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EPIDEMIOLOGY OF STEM RUST IN WESTERN CANADA[1]

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INTRODUCTION

Recurrent outbreaks of stem rust (*Puccinia graminis* Pers.) have been responsible during the present century for a great deal of damage to cereal crops in Western Canada, particularly to wheat. Although severe epidemics have occurred only periodically, yet the disease has been present every year and has caused a greater or less amount of damage. As a matter of fact, as early as the year 1896, it caused considerable damage in Manitoba (16). A heavy outbreak occurred in 1904, but it was not until 1916 that the loss caused by it reached calamitous proportions. In that year, the loss in wheat amounted to 100,000,000 bushels (29, 65, 189). Since then several other very destructive outbreaks have occurred, notably in 1923, 1927, 1935, and 1938. Calculations made recently (79) show that, for Manitoba and Saskatchewan, the average annual loss in wheat between 1925 and 1935 was in the vicinity of 35,518,000 bushels, and, in oats, for the 6-year period 1929-1934, around 8,334,000 bushels. For Manitoba, the yearly loss in barley between 1916 and 1937 was estimated at 2,350,000 bushels (44). Rye has never been injured to any appreciable extent. Within the last few years, losses from stem rust have been largely eliminated in wheat and oats by the extensive introduction of rust-resistant varieties of these two cereals.

As is well known, Western Canada is largely a cereal-producing area. Wheat is the most important crop, occupying a total of approximately 23,200,000 acres, 2,500,000 being in Manitoba, 13,200,000 in Saskatchewan, and 7,500,000 in Alberta. Approximately 9,500,000 acres are sown to oats, about one-half being in Saskatchewan, one-third in Alberta, and the remainder in Manitoba. Barley occupies a little in excess of 3,000,000 acres, about equally divided among the three provinces. Only about 700,000 acres are sown to rye, distributed among the three provinces in about the same proportion as given for oats.

Seeding and harvesting of wheat usually become general a week or more earlier in the southern than in the more northerly parts of the three provinces. The actual dates for seeding and harvesting vary a good deal with the season. Perhaps the last week in April and the second week in August may be taken as the usual time, respectively, when seeding and

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harvesting operations become general over the greater part of Western Canada. Barley and oats are generally regarded as of secondary importance, and are usually sown after most of the wheat seeding has been done. To some extent, harvesting of the three crops proceeds concurrently, but most of the barley is cut earlier, and most of the oats later, than the wheat. Rye is sown both in the autumn and in the spring, but all of it ripens about the same time, usually a little earlier than barley.

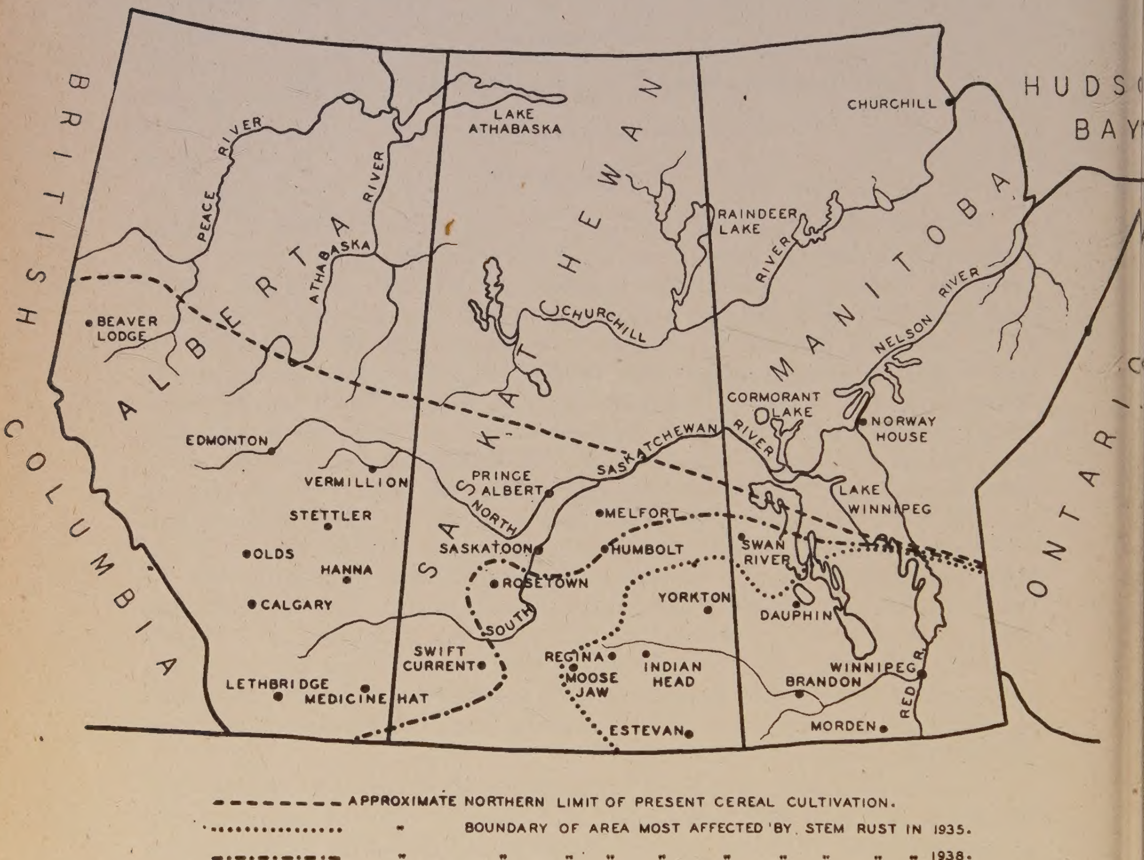

FIGURE 1. Map of Western Canada, showing the approximate northern limit of cereal production and the boundary of the area most affected by stem rust in 1935 and in 1938.

The area most frequently and most severely affected by stem rust embraces Manitoba and eastern Saskatchewan, the so-called "rust area." The western boundary of this area may be represented roughly by a line running northerly through Assiniboia, Moose Jaw, Humboldt, and Melfort, in Saskatchewan. Figure 1 indicates approximately the respective boundaries of the areas severely damaged in the stem-rust epidemics of 1935 and 1938. It also shows the approximate northern boundary of the cereal-growing area. Except in two or three of the epidemic years, western Saskatchewan and Alberta have sustained relatively little injury from stem rust. Broadly speaking, the general tendency in Western Canada has been for the severity and the frequency of stem-rust attacks to decrease

from east to west. Manitoba has suffered most from these attacks, Alberta the least; although not infrequently in Alberta late crops have been heavily rusted.

Three different varieties of stem rust occur on cereal crops in Western Canada. The variety that attacks wheat and barley (*Puccinia graminis Tritici* Erikss. & Henn.) is the most important. Barley, however, has never suffered so severely as wheat, for the bulk of this crop ripens earlier than the wheat and, on this account, has usually escaped the full force of severe outbreaks, although, in bad rust years, late barley has always been severely damaged. Next in importance comes stem rust of oats (*Puccinia graminis Avenae* Erikss. & Henn.). It has usually been severe in years when stem rust has been heavy on wheat, although this has not always been the case. For example, in 1937, infection on wheat was severe in south-central and central Manitoba and moderately severe in the eastern portion, but infection on oats was of no consequence. On the other hand, in 1932 and 1934, two non-epidemic years, oat stem rust was more prevalent than wheat stem rust. The third variety, stem rust of rye (*Puccinia graminis Secalis* Erikss. & Henn.), has never been of any importance. As a rule, little more than a trace of this rust has ever been found on the rye crop.

Purpose and Plan of the Investigation

As already stated, stem rust has been present every year in Western Canada since the beginning of the present century, but it has been more destructive in some years than in others. An investigation, extending over a period of years, has been made (a) to determine the source of the inoculum that yearly initiates stem rust in this area, (b) to detect each year the first appearance of the disease in the field, (c) to observe its subsequent rate of development and direction of spread, and (d) to ascertain if possible what factors promote or retard the intensity of its attack.

Some phases of the investigation were begun in 1918, but the bulk of the data presented in this paper has been accumulated since 1925. At the beginning of the investigation, relatively little was definitely known concerning the source of inoculum that initiated outbreaks of stem rust in this region, although three possible sources were recognized: (a) aeciospores from the common barberry, (b) uredial material that overwintered, and (c) wind-borne spores that originated in some other area. These three possibilities were studied with the view of determining to what extent each might be a contributory factor toward the establishment of primary infections in the new crop. In addition, field surveys were carried out each year to observe the progress of the disease and to determine the area affected by it. And, finally, meteorological data were studied to ascertain the influence of different meteorological factors on the development and spread of the disease.

Owing to the fact that spring wheat is the most important crop in Western Canada and the one most frequently and severely affected by stem rust, it was in this crop that the best sequence of observations were possible on the development and spread of the disease, and, consequently, the discussion in this paper deals principally with wheat stem rust (*Puccinia graminis Tritici*) in spring-sown wheat. As, in 1939 and subsequent years,

the area seriously affected by stem rust has been sown to stem-rust resistant varieties of wheat and oats, the data considered in this paper terminate with the year 1938.

Sequence in Time and Place of Early Infections

It will make possible a better understanding of the other aspects of the study if a general statement is first made as to the sequence in time of the first appearance of stem rust in different parts of Western Canada. The field surveys have shown that, year after year, outbreaks of stem rust follow the same general course of development, although the severity of the outbreaks may vary very markedly. Initial primary infections never become common in a district until after the crop, or a considerable part of it, in that district has headed or is coming into head. Almost without exception, the first traces of the disease occur in southern Manitoba, more often than not in the Red River Valley. About a week after the first traces appear, widely scattered pustules are usually found over most of the southern part of this province. Occasionally, however, as in 1929 and 1935, a uniform sprinkling of pustules may appear almost simultaneously over this whole area. In either case, the time of appearance is usually the last week of June or the first week in July. Further north, the disease makes its appearance somewhat later. For instance, in the Swan River Valley, the most northerly agricultural area in Manitoba, the advent of stem rust is usually from two to three weeks later than in the Red River Valley. In Saskatchewan, stem rust appears first, as a rule, in the south-eastern part, and from a few days to two weeks, or more, later than in southern Manitoba. Northward and westward, there is a progressive delay in the date on which stem rust first appears in the crop. As might therefore be expected, the disease usually reaches Alberta later than it does western Saskatchewan, and a month or more later than it does southern Manitoba. Table 1 gives the dates on which stem rust was first detected each year in the field in the three Prairie Provinces from 1926 to 1938.

Table 1.—Dates on which stem rust of wheat was first detected in the field in the three Prairie Provinces, from 1926 to 1938

Year	Manitoba	Saskatchewan	Alberta
1926	June 30	July 14	Aug. 17
1927	July 6	July 17	Aug. 15
1928	July 9	July 20	Aug. 21
1929	July 3	July 5	Aug. 23
1930	June 26	July 11	Aug. 10
1931	July 5	July 25	Sept. 5
1932	June 20	July 22	Aug. 12
1933	June 28	July 14	Sept. 8
1934	July 5	July 16	Aug. 4
1935	July 2	July 7	Aug. 15
1936	June 26	July 3	Aug. 6
1937	June 28	June 28	Sept. 3
1938	June 22	June 21	July 29

POSSIBLE SOURCES OF INFECTION

Infected Barberry as a Source of Infection

The common barberry (*Berberis vulgaris* L.) is the alternate, or secondary, host of stem rust (Figure 2). It is generally regarded as the principal source of the disease in areas where the winters are too severe to permit the survival of the uredial stage of the organism from one crop

Figure 2. Common barberry bush, the alternate host of the stem-rust fungus. (Courtesy of the United States Department of Agriculture).

season to the next, although wind-borne spores may be responsible in greater or less part for the initial infections in such areas and overwintering may occur in a few of them. Most of these areas lie in the north temperate zone, and include all or practically all European countries (5, 6, 12, 18, 27, 60, 77, 80, 87, 90, 100, 109, 116, 120, 121, 126, 145, 177, 178, 181, 182, 185,

190, and others), at least some parts of Eastern Asia (86, 173, 183), the northern United States (23, 57, 108, 113, 141, 144, 149, 165, 176, 189, 191, 205, 206, and others), and Canada (41, 95, 99, 146). In many of these areas, the eradication of barberry has greatly lessened the amount of infection from this source (27, 61, 80, 85, 88, 90, 119, 157, 190, 195, 211) and apparently in a few others barberry has never become established (68, 183). In warmer areas, barberry rarely becomes infected or is largely absent, and is consequently of little or no importance in the perpetuation of the disease from year to year (1, 30, 48, 72, 112, 113, 127, 131, 134, 138, 160, 161, 163, 206, 223, 229, 230). Where barberry is present in such areas, infection is largely or entirely prevented, apparently because the black spores are devitalized by the excessive heat of summer (31, 94, 113, 193, 206). In Argentina, barberry species may be of some importance as a source of infection (175), but to what extent they play a part in the origin and yearly survival of races of stem rust is not known (221).

In Western Canada, the common barberry was never extensively introduced. It was planted as an ornamental shrub in some of the cities and a few towns, but, in the country, the number of plantings was very limited. Following the epidemic of stem rust in 1916, the three Prairie Provinces, particularly Manitoba, commenced (1917) the eradication of this shrub, and most of the plantings were destroyed within the next few years. An Act passed by the Dominion Government in 1919 forbade the distribution and sale of barberry plants in these provinces, and authorized the eradication of all plantings. By 1925 the eradication was virtually completed (99), and since that time no new plantings have been discovered. Nevertheless, since that time three extremely destructive outbreaks of stem rust have occurred (1927, 1935, and 1938) and three of moderate severity (1925, 1930, and 1937). It would appear, therefore, that local barberry plantings were not a principal source of infection in Western Canada. In passing, it should be mentioned that, although the number of barberries in this area were few in comparison with the number in some other areas, those that were present did serve as distribution centers of early inoculum, and their eradication has, therefore, removed from the localities in which they were present a perennial source of infection.

Overwintered Rust as a Source of Infection

It is now quite well established that the stem-rust organism, in the absence or non-participation of its alternate host, the common barberry, is capable of surviving in the uredial (red) stage from year to year in certain parts of the world where climative conditions make the persistence of this stage possible. In other words, the red stage of the rust is said to overwinter (or "over-summer" in certain areas). This stage is known to persist throughout the year in Australia (40, 127, 128, 229, 230, 232), New Zealand (48), Kenya (30, 114, 217), Tunis (37, 160, 161), Italy (42, 184, 186), possibly in Portugal (19, 20) and Japan (86), in sub-tropical South America (72, 73, 74, 223), and in some districts in the Foothills of northern India (131, 132, 134, 135). In North America, it overwinters in some of the milder parts of the United States (85, 113, 189, 192, 193, 195), including the Pacific coastal region, some protected mountain valleys, and the Gulf States, and in southern and probably in northern Mexico (213).

But in other parts of the world where the winters are moderate to severe, this stage does not overwinter, or, at least, it overwinters to such a limited extent that its survival is a negligible factor in the annual recurrence of the disease. This is true of most countries of Europe (8, 55, 56, 59, 68, 75, 100, 109, 111, 126, 130, 133, 145, 172, 177, 178, 182), the Amur Region in Eastern Asia (173, 183), the northern half of the United States (33, 39, 91, 102, 153, 156, 157, 158, 165, 176, 189, 190, 193) and probably Eastern Canada. In the latter area, Fraser (64) found that a very low percentage of urediospores survived the winter in Quebec, but the possibility of stem rust overwintering has not been adequately investigated. In passing, it may be mentioned that, in certain areas, such as the Plains of India (31, 131, 132, 134, 135), the persistence of the uredial stage is prevented, not by winter conditions but by the intense heat of summer.

There are three possible ways in which the uredial stage of the stem-rust fungus may persist during the period between one crop season and the following one. It may persist (a) by successive infections, each new generation of spores giving rise to new infections, (b) by dormant mycelium in infected host tissue, or (c) by long-lived urediospores. The first possibility presupposes the presence of green susceptible plants and weather conditions suitable for infection. As, in Western Canada, the period between crop seasons includes five winter months during which all plant growth out-of-doors is suspended, there is no possibility of the fungus persisting, or overwintering, by means of successive infections. If, therefore, the fungus persists, or overwinters, at all, either the mycelium in infected plant tissue must be dormant throughout the winter and revive sufficiently in the spring to produce a new generation of spores, or urediospores produced in the previous season must remain alive through the winter and early spring until new growth of susceptible grass or grain is available for them to infect. Unless the fungus can establish new infections in the spring or early summer by one of these means, it cannot be said to overwinter.

Possibility of Overwintering by Means of Dormant Mycelium

The possibility of the uredial stage of stem rust persisting as dormant mycelium in host tissue throughout the winter in Western Canada is undoubtedly remote. In order that the fungus may survive as dormant mycelium, the host tissue that it pervades must itself remain alive, for, if the tissue were to die, the mycelium would be deprived of its source of nutrient supply and would die of starvation even though it did succeed in surviving the winter in a dormant condition. It would not, therefore, be able to develop and produce urediospores in the spring. It is by these spores alone that infection could spread from overwintered mycelium. Actually, at the beginning of winter, there is relatively little living plant tissue in which the fungus can have any chance of survival. All cereal crops are harvested in late summer or early autumn, and the stubble soon afterwards dies. No winter cereals are grown, except a relatively small acreage of winter rye in the three provinces, and a little winter wheat in southern Alberta. Frosts in late autumn and early winter kill practically all the native grass vegetation down to ground level before a covering of snow arrives to afford it protection. Only in an occasional sheltered

location do the basal leaves of any susceptible grass, such as wild barley (*Hordeum jubatum* L.), enter the winter in a living condition. The grass culms usually ripen and die long before winter sets in. Severe winter weather usually prevails from mid-November to early April, during which time the ground is continuously frozen and is usually covered with a light to moderate blanket of snow. During this period, all plant growth out-of-doors is suspended. No new grass vegetation appears until about the beginning of May, and, by the end of May, the spring-sown grain is little more than above ground.

Conditions between crop seasons are, therefore, wholly adverse to the survival of the rust during that period. As a rule, the earliest infections to appear in the new crop occur on wheat. If overwintering were to occur in winter rye, it would be expected that the first infections would appear on that crop or on nearby couch grass (*Agropyron repens* L.), a grass susceptible to rye stem rust. But this is not known to occur. Even if the mycelium were to persist in rye, infection could not spread from rye to wheat, as rye stem rust does not infect wheat. Overwintered mycelium in winter wheat in southern Alberta cannot be the source of early infection, as stem rust never appears there until late in the season, a month or more after it is present in the Red River Valley in Manitoba, 600 or 700 hundred miles distant.

Possibility of Overwintering by Means of Urediospores

How long urediospores can remain viable appears to depend a good deal on the conditions to which they are subjected after they are produced. DeBary (51) found that urediospores, when stored in the laboratory, lost their ability to germinate within 2 months. Schaffnit (180) obtained similar results with spores stored in the laboratory or out-of-doors in a sheltered location. In tests made by Jaczewski (100), spores collected on July 25 ceased to germinate 14 days later. When fresh spores, obtained artificially in October and November, were exposed to outside temperatures, germination ceased within 6 days. Sibilia (184) failed to obtain germination in urediospores after they were in storage for 20 or 22 days. From extensive tests, Hwang (97) came to the conclusion that the majority of urediospores in the air lose their vitality in from 12 to 14 days. Mehta (13) kept urediospores, which were produced in the greenhouse, in cold storage at a temperature of from 11.7° to 18° F. below the freezing point and found that, after 24 hours, less than 10% of them were capable of germination, and that after from 4 to 7 days none of them was germinable. Eriksson and Henning (59) found that urediospores stored in the open air during winter soon lose their power to germinate, but that unrediospores on straw stored in a room or laboratory, and thus protected from the vicissitudes of the weather, may retain their viability throughout the winter, a low percentage of such spores being capable of germination as late as May in the following spring. Pritchard (165) made various dispositions, both in the open and under cover, of sheaves of rusted straw that had stood in stook in the field until late autumn. By the end of September, germination was reduced to 2% and, by the middle of November, it had completely ceased. From the foregoing results, it would appear that, in urediospores, prolonged retention of viability is not generally the rule and that the period of viability may be markedly reduced by low temperatures.

Under constant environmental conditions, if they are at all favourable, urediospores may remain viable much longer than indicated above. Peltier (150, 152) stored urediospores under conditions of different constant temperatures and relative humidities and found that the longevity of the spores depended greatly on the combined influence of temperature and humidity. At the end of one year, he (152) obtained 30% germination in spores kept at a temperature of 41° F. and a relative humidity of 49%. At all humidities used, the longevity of the spores decreased as the temperature increased, and at all temperatures the spores remained viable longest at medium humidities. Raeder and Bever (168) found that the urediospores of stem rust retained their viability longer than those of stripe rust or of leaf rust of wheat, being viable at a relative humidity of 49% and at a temperature of from 48.2° to 55.4° F. for 128 days. In the laboratory, it has now become common practice to store urediospores of stem rust at a temperature of about 40° F. and a relative humidity of about 50%. Under these conditions, a high percentage of the spores remain viable for from 6 to 9 months.

The chances of urediospores surviving the winter in Western Canada are probably greatest for those spores that are produced late in the season. Such spores have at least the advantage that they are younger than those produced earlier and are exposed a shorter time to the vicissitudes of the weather. Moreover, if they are produced shortly before temperatures become too cool to permit spore production, they are probably better adapted to withstand low temperatures that occur before snow arrives to protect them. Melander (137) showed that urediospores that had been hardened by exposure for 10 days to temperatures just above the freezing point withstood exposures to temperatures of from −20° to −40° F. better than non-hardened spores, although very few spores of either class were able to survive long exposure to such low temperatures. Air temperatures of this order are not infrequent in Western Canada during the winter. Dry snow, however, is an effective insulator and, on days when such temperatures prevail, the temperature under a snow cover of 12 inches or more may be from 20° to 30° F. higher than the air temperature. At Winnipeg, in 1932, Thomson (216) found that, during January and February, the mean temperature of the surface soil under a snow cover was approximately 20° F., while on a few days during that period the air temperature dropped to −30° F. Under a cover of snow the spores are, therefore, afforded a considerable degree of protection from extremely low temperatures.

The critical periods for the spores are apparently early winter, before a snow cover is present, and late winter, after it has disappeared. During both these periods in Western Canada frosts and thaws may occur. Roussakov (172) pointed out that a cover of snow on frozen ground favoured overwintering but that light snow and thaws tended to prevent it. Lambert (113) expressed the opinion that, although urediospores may remain viable in the Upper Mississippi Valley throughout the winter, they are killed in the spring at the time of alternate freezing and thawing, as the spores, when moist, will germinate at temperatures below those at which infection can take place. The germ-tubes presumably either wither or are destroyed by frost.

It is possible, at least in some years, for urediospores to remain viable until late winter or early spring in the Upper Mississippi Valley and Western Canada. Bolley and Pritchard (24) found viable spores of stem rust on grass hosts frozen in ice in North Dakota in March, and Freeman and Johnson (67) found that in the winter of 1906-07 spores remained viable under snow at St. Paul, Minnesota, as late as the middle of April. In Manitoba, Jackson (98) collected germinable urediospores, usually from under snow, from October 15, 1919, to the middle of March in the following spring.

For several years, Fraser (66) made collections of urediospores from straw and dead grass in the spring. Most of these collections were made in northern Saskatchewan. Each spring, he found at least one collection that contained viable spores, but the proportion of such spores was usually low, about 1 or 2%; they were usually found beneath the leaf sheaths or glumes of the plants. The number of collections with viable spores was higher in 1922 than in the other years. In two of these collections made at Rosthern on April 24 and May 2, spores germinated to the extent of 6% and 10%, respectively. Spores from each collection were used to inoculate wheat seedlings, with the result that each collection gave rise to two infections, which developed into normal pustules. In the spring of 1929, Simmonds[3] made germination tests of urediospores collected on and beneath the leaf sheaths of wheat stems in a sheaf and in a straw pile that had been exposed to weather conditions throughout the preceding winter in the vicinity of Saskatoon. The collections were made on March 30, April 8, 16, 25, and May 4, the spores being taken from beneath leaf sheaths as well as from their outer surface. Eight collections gave positive, 9 gave negative results. In 6 of the 8 collections, there was little more than a trace of germination (0.1 to 0.3%). In the other two, made on March 30 and April 25, the percentage germination was 1.2% and 4.8%, respectively.

In the vicinity of Winnipeg, the usual experience is that urediospores on exposed surfaces of plants lose their viability before the severe winter weather sets in. This is particularly true of spores produced on plants that mature during the regular growing season. It is true also in some years, but not in all, of spores produced on very late sown experimental plots that are still green at the beginning of winter. In most years, spores on such plants lose their germinability completely by the middle of November, although, exceptionally, the majority of them may remain viable for a month later, and upwards of 10 to 15% as late as the beginning of the new year. In such cases, viability is largely or entirely lost by the end of January.

Spores produced in pustules beneath the leaf sheath of plants appear to have a much better chance of survival than those on exposed surfaces, for it is such spores that retain their viability longest, even in occasional years until late winter. By that time, however, traces only of germination have ever been found out-of-doors, and these only in extremely rate instances. Occasional collections of urediospores taken from beneath the sheaths of straw stored in sheaves in the laboratory barn have contained a trace of germinable spores as late as the first week of April, but not beyond that time. In one large pustule found beneath the leaf sheath of a wheat

[3] Unpublished data of Dr. P. M. Simmonds, Dominion Laboratory of Plant Pathology, Saskatoon, Sask.

plant, approximately 30% of the spores were found viable at the end of February. Part of this spore collection produced satisfactory infection on wheat seedlings. It would seem that, both under field conditions and under ordinary storage conditions in the vicinity of Winnipeg, urediospores of stem rust lose all viability before the beginning of May. At any rate, numerous germination tests on field collections of urediospores have been made at Winnipeg over a period of years during the first two weeks of May, but in no case have viable spores been found.

It must be admitted that the collections of spores tested for germination were made in a limited area, and the number of spores involved in the tests represented only an infinitesimal proportion of the number present in that area at the beginning of winter in any given year. Consequently, it would be hazardous to say that even here or elsewhere in Western Canada urediospores never survive later than the first week of May.

Probably the most likely place for the long survival of urediospores would be in stooks or stacks of unthreshed grain left in the field all winter. During the present investigation, a favourable opportunity was presented once for observing the result of having vast numbers of spores, produced in the previous year, liberated into the atmosphere during early summer. This happened in 1928. A severe epidemic occurred in 1927, and, as there was much rainfall during the summer and autumn, the crop matured exceptionally late, and harvesting was much delayed, so that in many areas a considerable amount of grain was left unthreshed in stook or in stack in the field during the winter. When seeding was finished in the following spring, threshing operations were resumed, and consequently many urediospores were thus liberated into the air during late May and early June. For example, slides exposed in south-eastern Saskatchewan indicated that there was a very considerable number of spores present at that time. Moisture conditions were favourable for infection, although the temperature in June was 2 or 3 degrees below normal, averaging about 57° F. This is too low a temperature for rapid rust development, but not too low for infection and slow rust development. It would be expected that, if infections did occur during late May and the first half of June and their development was retarded by the cool weather, they would have given rise to pustules when warmer weather arrived in late June and early July. Field infections might, therefore, have been expected to appear in this year as early as usual, or even earlier. Actually, however, the first infections appeared in the field later than usual, on July 9 in Manitoba and not until July 20 in Saskatchewan, a circumstance clearly due to the lack of viable inoculum in the early part of summer.

Infections of Doubtful Origin

It is true that one or two instances are known of stem rust being found present on a few wheat plants growing far distant from any other known field infections. The inference would naturally be that these infections had their origin in overwintered stem rust. One such case was found by Dr. G. B Sanford at Rosthern, Sask., on July 18, 1926. Secondary infections were present, so that probably the initial infection occurred about the first of July. Stem rust was first found in southern Manitoba on June 30 and in south-eastern Saskatchewan on July 14. A careful

search for infections on grasses growing in the vicinity of Rosthern was made by Dr. Sanford, but none was found. As wind-borne spores were present during the last week of June in south-eastern Saskatchewan, there is the bare possibility that some of these spores were carried as far north as Rosthern, although none were detected at that time on the slides exposed at Saskatoon, about 40 miles farther south. If that happened, such spores were probably responsible for the initial infection. A light rain fell in northern Saskatchewan on June 28, so that conditions for spore germination were probably more favourable there than in southern Saskatchewan where the weather during the last week of June was warm and dry. Whatever may be the correct conclusion concerning this case, and one or two other doubtful ones, the evidence is not conclusive that the rust overwintered.

Actually, the survival of urediospores during the winter is of no significance with respect to the overwintering of stem rust unless the spores remain viable far enough into the spring to permit infection in the new growth of grasses or in the young cereal plants. If overwintering of stem rust does occur, one would expect to find infections on susceptible grasses earlier in the season than on cereal crops; for, with the grasses, the new growth occurs in immediate proximity to the plants on which the disease was present in the previous year and in or on which the fungus might be expected to overwinter. Furthermore, new growth usually appears earlier in the grasses than in the cereals, and hence presents an opportunity for earlier infection. It is, therefore, rather surprising that, although during the last 21 or 22 years careful observations have been made on grasses in Western Canada by different workers, infection has scarcely ever been found on them earlier than on cereals, and never under circumstances which would give grounds for the suspicion that the infections arose as a result of the overwintering of the fungus. From a consideration of the evidence available, it must be concluded that overwintering is not a significant factor in Western Canada in the initiation of stem-rust infections in cereal crops, although the possibility of some infections arising from this source in an occasional year cannot be categorically denied.

Wind-Borne Spores as a Source of Infection

The importance of wind-borne[4] spores in the initiation of stem-rust epidemics is now well established for certain cereal-producing areas. In such areas as the Amur region in Eastern Asia (183), the Plains of India (31, 131, 132, 134, 135), and the Cape Province, South Africa (223), where stem rust is not known to survive in its uredial stage from year to year and susceptible species of barberry are not present, initial infections are dependent entirely on wind-borne spores. Probably the same is true of Egypt (138, 163). In areas where susceptible species of barberry are present, there is always some difficulty in determining to what extent wind-borne spores—as opposed to spores produced on barberry locally—are responsible for early infections, or how much infected barberry contributes to the development of an epidemic. Such an area is the Upper Mississippi Valley in the United States. There is considerable evidence that here, in some years at least, inoculum is carried by air currents from southern to

[4] The dissemination of rust spores is, under natural conditions, almost wholly by winds, or air currents, so that practically all spores might be designated as wind-borne; but, in this paper, the term is applied to spores that are transported by winds, or air currents, relatively long distances.

northern States (67, 93, 94, 113, 156, 157, 158, 192, 193, 195, 198, 209, 226). Apparently in early summer there is the possibility that upper air currents (4,000 feet elevation) over the United States may carry spores from New York, Pennsylvania, and other eastern States to Texas, Oklahoma, and Kansas, as well as from the latter States northward and eastward (93). It appears that, in South-eastern and Central Europe, also, there is, in addition to inoculum from barberry, a northward drift of inoculum, at least in some years, and outbreaks of stem rust have been attributed, in part at least, to wind-borne spores (12, 69, 178, 179, 181, 182, 187). Even in Australia, a country in which stem rust survives in the uredial stage from year to year, there is a drift of spores from the earlier, more northerly grain-growing areas to the later areas further south (232). A review of the literature relative to the aerial distribution of *Puccinia graminis* and other plant pathogens is given in a previous paper (45).

To gain information as to the part that wind-borne spores play in the initiation and subsequent spread of stem rust in Western Canada, a study was undertaken to ascertain the relative prevalence of spores in the air at different points during the summer months. For this purpose, use was made of glass slides exposed near ground level and during aeroplane flights. If stem-rust spores could be detected in the air at least a week or two earlier than infections occurred in the field, there would be, in the absence of any known local source of inoculum, strong circumstantial evidence that the early infections at least were caused by wind-borne spores.

Evidence of Stationary Slide Exposures[5]

The exposure of glass slides or Petri dishes, or the use of special devices to detect micro-organisms in the air has been resorted to at one time or another by different investigators. Owing to the facility with which they can be exposed and examined, glass slides have been much used. As early as 1882, Ward (228), in his study of the coffee rust, exposed slides coated with vaseline; and, in 1886, Millardet, according to Ducomet (54), exposed slides smeared with oil, and found that within a period of 24 hours as high as 32,000 mildew spores fell on 1 square decimeter of surface. Much information concerning the spread of cereal rusts has been procured by means of the slide-exposure method, particularly by Stakman and others associated with him (192, 193, 196, 202, 203) in epidemiological studies of stem rust in the Mississippi Valley, and by Shitikova-Roussakova (183) in the Amur Region of Eastern Asia. Others (2, 38, 67, 72, 100, 110) have adopted different devices to detect rust spores in the air.

In the present study, microscope slides smeared on one side with vaseline were exposed in a weather-vane type of spore-trap (Figure 3) at selected stations in each of the three Prairie Provinces. After exposure, the slides exposed in Saskatchewan and Alberta were returned to the Saskatoon Laboratory, and those exposed in Manitoba to the Winnipeg Laboratory, where they were examined under the microscope (Figure 4) and a record was made of the number of spores present on 1 square inch of slide surface. At some stations the slides were exposed for 24 hours, at others for 48 hours, and at two or three others for a somewhat longer time.

[5] This phase of the work was a co-operative study carried on by the Dominion Laboratory of Plant Pathology, Saskatoon, Sask., and the Dominion Laboratory of Plant Pathology, Winnipeg, Man.

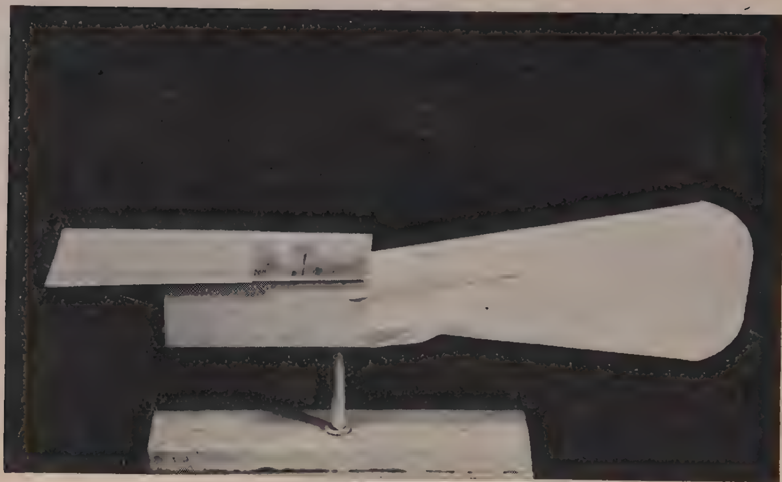

FIGURE 3. Stationary spore-trap, consisting of a galvanized sheet-iron case with sliding top and weather-vane tail, supported on a short iron shaft about which the trap can freely rotate. The slide is held in a vertical position, approximately equidistant between the top and bottom, by means of two U-shaped fixtures, one of which is soldered to either side of the trap.

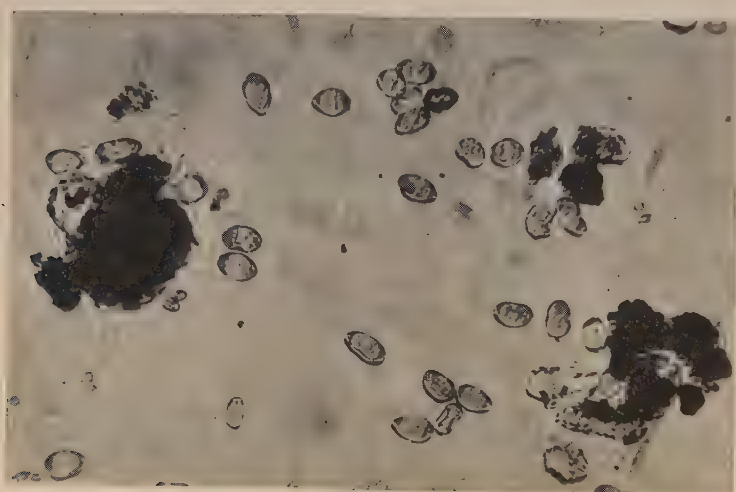

FIGURE 4. Urediospores of stem rust on a vaselined slide that was exposed in a stationary spore-trap for 24 hours at Winnipeg during the height of the 1935 stem-rust epidemic. Magnification, 120 app.

At most of the stations the exposures were begun on June 1, but at some, particularly in Alberta, where stem-rust infection appears late in the season, exposures did not commence until July 15. As a rule, the exposures were discontinued at the end of August. From 1926 to 1929, exposures were made at 5 stations in each province, but after 1929 the number of stations was reduced. Those at which exposures were made each year during the whole period 1926-1938 are as follows: Morden, Winnipeg, Brandon, in Manitoba; Indian Head and Saskatoon, in Saskatchewan; and Edmonton, in Alberta (Figure 1).

TABLE 2.—NUMBER OF STEM RUST UREDIOSPORES INTERCEPTED EACH 2-DAY PERIOD BY 1 SQUARE INCH SURFACE OF GLASS SLIDE EXPOSED AT MORDEN, WINNIPEG, AND BRANDON, MAN., AND INDIAN HEAD AND SASKATOON, SASK., FROM JUNE 11 TO JULY 20 EACH YEAR, EXCEPT 1936, FROM 1926 TO 1938

—	1926					1927					1928					1929				
	Morden	Winnipeg	Brandon	Indian Head	Saskatoon	Morden	Winnipeg	Brandon	Indian Head	Saskatoon	Morden	Winnipeg	Brandon	Indian Head	Saskatoon	Morden	Winnipeg	Brandon	Indian Head	Saskatoon
June 12	0	0	0	0	0	0	0	0*	0	–	0	1	–	0	–	0	0	0	2	1
June 14	0	0	0	0	0	0	3	0	0	–	0	0	–	1	–	0	0	0	1	0
June 16	0	0	0	0	0	0	1	0	–	–	0	0	0	2	1	24	133	0	0	0
June 18	0	0	0	0	0	0	0	0	0	5	0	0	1	3	2	174	193	68	0	0
June 20	0	0	0	0	0	0	0	0	2	13	0	0	0	4	2	0	0	0	0	0
June 22	0	0	0	0	0	0	2	4	0	0	0	0	0	0	0	0	0	0	0	0
June 24	0	0	0	1	0	0	3	3	0	0	0	0	2	1	0	0	0	0	2	0
June 26	2	3	0	2	0	5	31	0	0	0	1	0	1	2	1	0	0	0	1	24
June 28	5	0	0	3	0	9	20	0	0	0	0	1	0	1	3	15	1	0	2	0
June 30	0	0	0	3	0	0	4	0	1	0	0	0	0	4	7	0	0	0	1	0
July 2	0	0	0	0	0	0	0	5	2	1	0	0	0	0	0	1	0	0	1	1
July 4	0	2	0	0	0	13	38	9	0	36	0	0	0	4	0	1	2	2	0	0
July 6	0	1	0	1	0	7	22	0	0	2	0	0	0	11	2	0	4	0	1	4
July 8	0	4	0	2	0	0	18	36	0	0	0	0	1	0	7	0	3	1	16	1
July 10	1	1	0	1	0	8	0	–	0	0	0	0	2	0	2	3	481	0	5	2
July 12	3	2	0	1	0	0	4	–	0	2	0	2	0	6	0	1	283	0	1	3
July 14	64	24	0	1	0	5	3	22	0	0	0	45	3	8	1	2	31	0	2	–
July 16	152	5	0	8	1	7	1	7	0	0	0	0	0	8	7	3	117	0	4	2
July 18	980	15	4	1	3	0	10	3	1	0	1	4	2	3	11	3	37	5	6	1
July 20	945	0	1	7	2	9	254	2	15	0	2	6	5	8	3	199	2983	26	22	–

	1930					1931					1932					1933				
June 12	0	0	0	0	0	0	0	3	0	0	0	6	4	0	0	0	2	0	0	0
June 14	0	0	0	0	0	0	0	2	0	0	3	4	5	0	0	0	0	6	0	0
June 16	0	1	0	0	0	0	2	3	0	0	2	3	3	0	0	0	0	0	0	0
June 18	0	1	0	0	0	0	1	0	0	0	3	0	9	0	0	0	0	0	0	0
June 20	1	1	0	0	0	0	0	1	0	0	1	0	4	0	0	0	0	0	0	0
June 22	0	1	1	0	0	1	1	7	0	0	1	1	3	0	0	0	0	0	20	2
June 24	0	2	0	0	0	0	0	9	0	0	1	1	1	0	0	0	1	0	0	0
June 26	0	0	0	0	0	3	0	1	0	0	1	0	0	0	0	0	1	0	0	0
June 28	2	0	1	0	0	5	2	2	0	0	1	0	1	0	0	2	2	0	4	0
June 30	1	0	1	0	0	0	2	2	0	0	4	1	0	0	0	0	0	0	8	4
July 2	0	9	6	11	4	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
July 4	0	7	15	4	0	2	0	0	0	0	1	0	1	0	0	0	0	2	0	0
July 6	1	0	0	7	0	0	0	8	0	0	0	0	8	1	0	0	0	0	0	0
July 8	7	8	–	1	3	0	3	0	0	0	4	8	12	3	2	0	0	2	4	0
July 10	0	5	0	1	101	22	21	9	0	0	0	1	4	0	2	1	0	1	4	0
July 12	111	8	–	9	2	39	0	52	0	0	4	10	1	15	0	2	2	0	4	0
July 14	22	178	1	28	6	36	2	1	0	0	59	3	7	9	15	2	2	0	0	0
July 16	171	659	74	19	0	–	8	11	0	0	8	4	8	0	0	0	1	0	0	0
July 18	92	7	1	18	1	207	0	2	61	0	271	22	1095	94	0	2	5	9	0	0
July 20	–	32	112	168	0	27	9	10	11	11	117	93	18	22	0	20	10	12	0	0

* In 1927, the slides were exposed at Killarney, Man., up to July 8, and at Brandon from July 13, onward.

TABLE 2.—NUMBER OF STEM RUST UREDIOSPORES INTERCEPTED EACH 2-DAY PERIOD BY 1 SQUARE INCH SURFACE OF GLASS SLIDE EXPOSED AT MORDEN, WINNIPEG, AND BRANDON, MAN., AND INDIAN HEAD AND SASKATOON, SASK., FROM JUNE 11 TO JULY 20 EACH YEAR, EXCEPT 1936, FROM 1926 TO 1938—*Concluded*

—	1934					1935					1937					1938				
	Morden	Winnipeg	Brandon	Indian Head	Saskatoon	Morden	Winnipeg	Brandon	Indian Head	Saskatoon	Morden	Winnipeg	Brandon	Indian Head	Saskatoon	Morden	Winnipeg	Brandon	Indian Head	Saskatoon
June 12	0	0	0	0	0	0	0	0	0	0	1	4	0	0	0	1	0	1	0	0
June 14	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	29	5	8	0	0
June 16	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	18	0	0	0	0
June 18	0	2	0	0	0	0	0	2	0	0	1	2	0	0	0	29	0	0	0	0
June 20	0	2	0	0	0	0	0	0	0	0	1	2	0	0	0	43	18	9	0	0
June 22	0	3	1	0	0	0	0	0	0	0	2	8	7	0	0	3	10	0	0	0
June 24	0	0	0	0	0	22	249	6	0	0	2	13	–	0	0	10	0	2	0	0
June 26	0	2	0	0	0	6	52	3	0	0	0	2	–	0	0	1	1	2	0	36
June 28	0	1	0	0	0	0	10	0	12	0	0	1	0	0	0	18	86	17	84	0
June 30	0	0	0	0	0	84	54	31	12	0	2	0	0	0	0	59	328	2	4	0
July 2	0	0	0	0	0	61	29	22	0	0	0	0	1	0	0	25	5	7	12	0
July 4	0	0	1	0	0	9	19	7	0	0	18	1	–	24	0	23	0	2	0	–
July 6	3	0	0	0	0	4	5	0	19	0	110	190	80	0	0	14	4	5	18	12
July 8	13	15	16	9	0	11	1	0	0	0	10	3	1	0	4	580	3	81	126	0
July 10	0	3	10	5	0	33	3	23	0	0	125	82	3	5	15	900	140	224	432	0
July 12	6	1	0	0	0	195	15	23	11	0	170	0	4	32	0	6120	247	430	1204	80
July 14	8	9	2	0	0	–	13	9	10	0	100	13	48	0	0	9420	113	395	810	160
July 16	64	4	2	58	8	–	1175	16	7	6	8	2	38	48	0	3540	390	360	1015	0
July 18	36	1086	7	11	0	–	385	73	21	4	3300	44	210	0	0	810	880	490	1524	50
July 20	17	1	3	47	29	3620	504	595	450	5	6000	232	630	0	0	146	200	595	72	4230

* In 1927, the slides were exposed at Killarney, Man., up to July 8, and at Brandon from July 13, onward.

No one needs to be reminded that "the wind bloweth where it listeth," and, as a consequence, no great regularity could be expected with respect to time and place of the first appearance and number of spores on the slides. Moreover, the location of the station, whether in a depression or in an exposed area, and the actual location of the spore-trap at the station, no doubt influenced to some extent the number of spores that came into contact with the slides. Furthermore, it is almost too much to expect that a small glass slide would detect the first spores to arrive in any district. On the assumption that spores in the first 1,000 feet of atmosphere are uniformly distributed, the presence of 1 spore on 1 square inch of slide exposed for 24 hours would indicate that somewhat more than 760,000,000 spores had passed through a vertical plane extending laterally 1 mile and to a height of 1,000 feet. The fact, however, that 1 spore on a slide may indicate the presence of such a large number in the atmosphere gives added significance to the low number of spores on some of the slides (Table 2). With a lesser number of spores present, a slide might or might not detect them. At best, therefore, the data furnished by the slides can only be regarded as an indication of the relative number of spores present and an index, possibly, of the dates on which the number was in excess of the minimum usually necessary for detection. For the same reason, the dates

on which 1 or more spores were first detected by slides exposed at different stations do not necessarily indicate the earliest dates on which spores were present in the atmosphere over the districts represented by the stations.

Number of Spores Intercepted. Data collected during the 13-year period 1926 to 1938 on the daily number of spores intercepted, if presented with any degree of completeness, would occupy an undue amount of space, and no very satisfactory scheme has been found of summarizing them in the form of a table. A part of the data is contained in Table 2, which gives the number of urediospores of stem rust per square inch intercepted each 2-day period by slides exposed at Morden, Winnipeg, and Brandon, in Manitoba, and Indian Head and Saskatoon, in Saskatchewan, between June 11 and July 20 for the period 1926-1938 (except 1936, a light rust year, which is omitted to conserve space). As at Edmonton practically no spores were intercepted by the slides exposed before July 20, the results for that station are omitted entirely. The interval from June 11 to July 20 was selected for the reason that before June 11 very few spores were intercepted by the slides at any of the stations and after July 20 locally produced spores were usually becoming so plentiful, particularly in southern Manitoba, as to cause an appreciable increase in the number of spores intercepted by the slides, and thus to obscure evidence of low to moderate influxes of wind-borne spores. It is not proposed to discuss at this point the data presented in Table 2, as these data will be drawn upon in different parts of the subsequent discussion. Attention, however, may be called to the occasional sudden increases in the number of spores intercepted by the slides at one or more of the stations, followed usually within 2 or 3 days by an equally sudden decrease. These sudden increases in the spore population of the atmosphere constitute the so-called "spore showers," and they have an intimate relation to the development of stem rust in the areas where they occur.

Viability of Early Spores. In regard to the viability of the early arriving spores, it may be said that any spores intercepted during the first week of June in any year were generally somewhat bleached in appearance, and failed to germinate when the slides bearing them were placed under conditions favourable for germination. There is not much likelihood that such spores were capable of causing infection, although it should be mentioned that germination tests of viable-looking spores somewhat later in the season were not very successful, probably because the spores became embedded in the vaseline—a circumstance that prevented their contact with water when they were placed in a saturated atmosphere. From time to time, however, germination was secured; and, in fact, occasionally during humid weather, the spores on some slides germinated while the slides were yet exposed.

To remove any uncertainty as to the viability of spores found in the atmosphere before infections appeared in the field during the later years of the investigation, a different method was adopted. An attachment, which accommodated and held firmly the bottom of a Petri dish, was fastened to an automobile in such a manner as to hold the Petri dish bottom in a vertical position and facing in the same direction as the automobile. When a survey trip during the latter part of June was to be made, a thin fresh layer of plain agar was poured over the bottoms of several dishes and

the covers replaced. The dishes were taken along on the trip, and from time to time one of them was exposed by removing the cover and fixing the bottom to the attachment. Not infrequently the spores germinated before the dishes could be brought back to the laboratory and examined. The results obtained by this method showed clearly that, from 1931 to 1938, viable spores were present in Manitoba for a week or two each year before any infections occurred in the field.

Relation of Data to Pattern of Rust Development in the Field. In spite of the evident limitations of the slide-exposure method, the data obtained through the exposure bear a generally recognizable relationship, at least in most years, to the broad pattern of stem-rust development and spread in different parts of Western Canada. For instance, it will be seen from Table 3 that spores in detectable concentrations were present at Morden and Winnipeg, Man., usually earlier than at Indian Head, Sask., always considerably earlier than at Saskatoon, Sask., and generally a month or more earlier than at Edmonton, Alta. It will be recalled (Table 1) that a similar westward lag occurred in the first appearance of field infection. Infections appear on the crops in southern Manitoba from a few days to upwards of a month earlier than in Saskatchewan, and from a month to two months earlier than in Alberta.

Furthermore, a comparison of Tables 1 and 3 will show that, as a rule, stem-rust urediospores were present in the atmosphere at the different stations in Manitoba and Saskatchewan from a few days to a week or more before any infections occurred in the field, and in Alberta generally for a much longer time. The two or three evident exceptions can be explained by the fact that, in Table 1, the dates on which the first infections appeared in a province apply to the province as a whole, no matter where the infections occurred. For example, in 1926, the first infections on wheat in Alberta appeared on August 17 but spores were not detected by the slides exposed at Edmonton until August 24. However, slides exposed at Lethbridge and Olds, Alta., detected spores on August 10 and 13, respectively, so that spores were present in the province at least a week before any infections were found in the field. Or again, in 1938, the spore shower that occurred in Manitoba on June 13 and 14 reached the eastern margin of Saskatchewan but did not extend as far west as Indian Head. No spores were intercepted at that station until towards the end of June, but infections appeared along the eastern edge of the province as early as June 21. Infections were, therefore, present in the crop about a week before spores were intercepted by the slides exposed at Indian Head. Apparently, however, the slides exposed at Indian Head in 1937 failed to detect spores in the air before infections appeared in the field, for a few infections were found at that station on June 28, but no spores were detected by the slides until July 4. Spores, however, were present in the air over Manitoba considerably earlier, for a well defined spore shower occurred on June 13 and 14. This seems to be the only instance where, in a particular locality, the slides failed to detect the presence of spores before infection appeared in the field.

TABLE 3.—DATES ON WHICH STEM-RUST SPORES WERE FIRST DETECTED ON SLIDES EXPOSED AT MORDEN, WINNIPEG, INDIAN HEAD, SASKATOON, AND EDMONTON, FROM 1926 TO 1938

Year	Morden	Winnipeg	Indian Head	Saskatoon	Edmonton
1926	June 4	June 5	June 24	July 16	Aug. 24
1927	June 25	June 1	June 19	June 17	Aug. 3
1928	June 5	June 6	June 2	June 16	July 20
1929	June 16	June 7	June 12	June 4	July 23
1930	June 6	June 9	July 1	July 1	July 27
1931	June 6	June 9	July 17	July 19	July 18
1932	June 7	June 3	July 5	July 7	July 27
1933	June 28	June 12	June 29	June 21	Aug. 11
1934	July 7	June 10	July 7	July 14	July 29
1935	June 6	June 19	June 26	July 17	Aug. 4
1936	June 2	June 3	June 21	June 23	July 20
1937	June 9	June 1	July 4	July 8	Aug. 9
1938	June 3	June 1	June 28	June 26	July 15*

* Spores were present on the first slide exposed (July 15).

It would not be expected that the earliest arriving spores generally produced infections. As a matter of fact, in some years, as much as three or four weeks elapsed between the first trace of spores on the slides and the earliest occurrence of field infections. The occurrence of infection, of course, depends on the viability of the spores themselves and on weather conditions after their arrival. How soon, after infection takes place, pustules appear on the plants depends largely on subsequent temperature and light conditions. It is improbable that the stage of crop maturity influences the course of rust development. These aspects will be considered in later sections of this paper. What is worthy of notice here is that, in every year of the investigation, spores were almost invariably present on the slides exposed in each of the three provinces before any infections could be found on the crops or native grasses. It is, therefore, reasonable to conclude that the wind-borne spores were responsible for the infections.

Long-Distance Spore Dissemination. From the slide-exposure studies, many instances could be cited of the long-distance dissemination of stem-rust spores, but two or three will suffice. In 1927, the slide exposed at Beaver Lodge in the Peace River Valley, Alberta, during the week ending July 28 intercepted 3 urediospores per square inch. No spores were found for the next two weeks, but the slide exposed during the week ending August 18 intercepted 77 spores per square inch. Up to 1927, stem rust was unknown in the Peace River Valley, and it was not reported again until 1938. It is, therefore, most improbable that these spores were of local origin. Rather would it appear that they had come from areas quite far distant. Field infections only began to appear in the vicinity of Edmonton after the middle of August, and, at the end of July, were largely confined to eastern Saskatchewan, so that the spores found at the end of July at Beaver Lodge probably did not originate nearer than eastern Saskatchewan or the International Boundary, and those found at the middle of August, nearer than western Saskatchewan, distances, respectively, of at least 700 and 300 miles.

In 1929 a heavy spore shower occurred during June 16 and 17 in southern Manitoba. It was heavier at Morden and Winnipeg in the eastern part of the province than at Brandon in the western part, and it did not extend as far west as Indian Head and Saskatoon. No infection was present in Western Canada, and, according to information received from the United States Department of Agriculture, the northern limit of stem-rust infection in the Mississippi Valley on those dates can be indicated by a curved line passing through central Colorado, northeastwardly through Nebraska into south-eastern South Dakota, and thence south-eastwardly into central Illinois. Only traces of stem rust were present along this northern boundary. At Winnipeg, however, the slide exposed on June 16 intercepted 133 spores and the slide exposed on June 17 intercepted 193 spores per square inch. At two or three other points in eastern Manitoba, comparable numbers of spores were intercepted on June 17. Evidently these spores must have originated somewhere south of the line previously mentioned, and must have, therefore, been carried northward for 500 miles or more. Practically no spores were intercepted on June 18, although throughout the day the wind continued in the same direction. Apparently most of the spores were washed out of the air by rain that occurred on that date from eastern Nebraska northward to Manitoba.

The epidemic of 1935 offers another example of the long-distance spread of stem-rust spores. The first spore shower of that summer occurred during a period of south wind, from June 23 to 25. The shower was quite heavy, for the slide exposed at Winnipeg on June 24 intercepted 240 urediospores per square inch. Stem rust was then just appearing in the southern part of Minnesota and South Dakota[6], a distance of approximately 400 miles from Winnipeg. As at that time only a trace was present in those areas, it is very probable that the spores reaching Winnipeg originated still farther south, and, consequently, the distance travelled by them was perhaps considerably greater than that just indicated.

That urediospores of stem rust are carried far north beyond the cultivated region of Western Canada is indicated by the fact that Newton, late in the summer of 1936, found stem rust on volunteer wheat plants growing at Churchill on Hudson Bay, about 600 miles north of Winnipeg (144); and, in September, 1940, on *Hordeum jubatum* at Hay River, on the western end of Great Slave Lake, about 500 miles north of Edmonton[7]. Churchill is about 500 miles from the nearest cereal-growing area, and Hay River about 350 miles. The probability is that, in both instances, the infections were caused by wind-borne spores. Several times during the summer of 1936 the high and low air-pressure areas (See page 000) were in a favourable position to bring spores by a southerly wind to Churchill from infected grain-growing areas. Slides exposed at Norway House, 275 miles north of Winnipeg, have shown that spores in large numbers (Table 4) are sometimes present in the air that far north, and it is probable that spores in considerable numbers are occasionally carried as far north as Churchill,

[6] Compare U.S.D.A. Plant Disease Reporter 19 : 154. 1935.

[7] Newton, Margaret. Additions to the fungus flora of the McKenzie River Basin. *In* Annual Report of the Canadian Plant Disease Survey, 1940. Division of Botany and Plant Pathology, Canada Dept. Agr., Ottawa 20 : 100-102. 1941.

or even farther. It would seem probable, too, that, in 1940, spores from the grain-growing area of Western Canada were carried north-westerly as far as Great Slave Lake.

Evidence of Aeroplane Slide Exposures

In addition to the stationary exposures, slides were exposed during aeroplane flights. The purpose of these exposures was to supplement the data furnished by the stationary slides and to give some indication of the concentration of spores in the air at different altitudes, as well as to ascertain whether or not they were present over northern areas where it was not possible to expose stationary slides. It was only through the generous co-operation of the Branch of the Royal Canadian Air Force stationed at Winnipeg that this phase of the work was made possible. These exposures were continued from 1925 to 1931. An account of each year's results is contained in the Reports of the Dominion Botanist, Department of Agriculture, Canada, for those years, and, consequently, a discussion of the results obtained need not be given here in detail.

A considerable number of studies have been made by different investigators to gain information concerning the fungal and bacterial population of the atmosphere, and a good deal has been learned concerning the identity of the organisms present and their relative numbers. Reference to such studies has been made in another publication (45). From them it is evident that micro-organisms may be present even to a height of three miles or more above the surface of the earth, although at high levels they are very much less numerous than at lower levels. Stakman, Henry, Curran, and Christopher (203), in an attempt to discover to what height stem-rust spores were present in the air over different parts of the Mississippi Valley, found various kinds of spores up to an altitude of 16,500 feet—the highest level at which exposures were made. Urediospores of stem rust caught at 7,000 feet germinated readily. These investigators used several different types of spore-trap, one of which was adopted for the present work.

In the present work, the exposures were made largely during forest-patrol flights in Manitoba, in the months of July and August, but not according to any definite schedule. The duration of most of the exposures was 15 minutes, but some slides were exposed for only 5 or 10 minutes. Each exposure was made at a definite altitude, the range being from 1,000 to 7,000 feet. In Manitoba, exposures were made from 1925 to 1929 over areas lying east of the southern extremity of Lake Winnipeg, and others over areas at the northern extremity of Lake Winnipeg, and, from 1926 to 1929, in the vicinity of Cormorant Lake, about 90 miles west-by-north of the latter locality. No exposures were made in Saskatchewan, but some were made at High River, Alberta, in 1925 and 1926. The type of spore trap used is illustrated in Figure 5.

As the slides were exposed for a relatively short time, it would appear that spores would have to be fairly plentiful in the air before any considerable number of them would be intercepted during an exposure. As a matter of fact, the number was usually low, particularly on those slides exposed in late June and early July. On many of these no spores were found at all. Later in the season, however, the number occasionally was surprisingly high. For the purpose of this study, the exposures of most

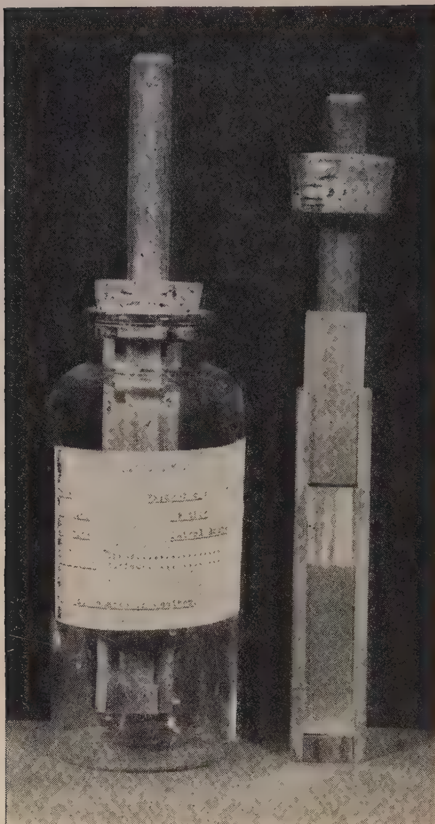

FIGURE 5. Spore trap used in making slide exposures during aeroplane flights. Two glass slides placed end to end are held in position on the front side of a wooden paddle by means of two narrow grooves that face inwards. A thin smear of vaseline covers the exposed face of each slide. The handle of the paddle projects through a perforated stopper that fits tightly into the mouth of the bottle. For an exposure, the paddle is removed from the bottle and held with the slide facing in the direction of flight for a designated length of time.

interest are those made at Cormorant Lake. This lake is more than 300 miles north of Winnipeg and is separated from the nearest cultivated area by a region of forest and lakes approximately 150 miles in width.

Northward Dispersal of Spores. The results of the exposures in the Cormorant Lake region are given in Table 4, and furnish some evidence of distant northward dispersal of stem-rust spores. Relatively few spores were intercepted by the slides exposed in 1926, a light rust year, but in 1927, a year of late crops and heavy stem rust, spores in this region were much more numerous. The number was considerably less in 1928 and in 1929, both comparatively light rust years.

It cannot be said with absolute certainty that these spores were not of local origin, as Cormorant Lake is not easily accessible, except by aeroplane, and no observations were made to determine whether or not stem rust was present on native grasses growing in the vicinity. There is little likelihood, however, that such a high concentration of spores in the air, as indicated by

the number on some of the 1927 slides, could have originated locally, if, indeed, any local infection was present at all. Rather would it appear that the source of these spores was the rusted grain fields of southern Manitoba. In 1928, stem-rust spores were caught by the exposures made between July 13 and 19. The first traces of stem rust in the field appeared in the southern part of the province between July 9 and 12. These few scattered pustules would be entirely inadequate to produce sufficient inoculum to account for so many spores being present in the air more than 300 miles distant. There can scarcely be any doubt that they originated south of the international border. The high and low air-pressure areas (to be discussed later) were so positioned on July 13 and particularly on July 14 as to bring a south wind to northern Manitoba, a fact that seems to support this belief. The same is true of July 29 and August 5, on which 21 and 15 spores, respectively, were intercepted by the slides. In general, it would appear that, when any considerable number of spores were intercepted in that region, their presence may be attributed to dispersal by south winds.

TABLE 4.—THE NUMBER OF STEM-RUST UREDIOSPORES PRESENT PER SQUARE INCH ON GLASS SLIDES EXPOSED FOR 15 MINUTES DURING AEROPLANE FLIGHTS AT CORMORANT LAKE, ON THE DATES INDICATED, AT ALTITUDES BETWEEN 3,000 AND 5,000 FEET

1926	1927	1928	1929
July 12 – 0	July 7 – 0	July 13 – 4	July 13 – 0
July 15 – 0	July 12 – 0	July 14 – 7	July 18 – 0
July 17 – 0	July 17 – 0	July 16 – 2	July 19 – 1
July 24 – 0	July 23 – 0	July 19 – 18	July 20 – 1
July 25 – 1	July 25 – 1	July 27 – 0	July 21 – 0
July 29 – 0	July 29 – 0	July 28 – 0	July 25 – 0
		July 29 – 21	July 28 – 0
		July 30 – 0	July 29 – 1
			July 30 – 0
Aug. 3 – 1	Aug. 11 – 13	Aug. 5 – 15	
Aug. 10 – 0	Aug. 12* – 89	Aug. 8 – 0	Aug. 1 – 4
Aug. 14 – 2	Aug. 12* – 45	Aug. 10 – 0	Aug. 3 – 0
Aug. 17 – 2	Aug. 12* – 3	Aug. 18 – 1	Aug. 4 – 1
Aug. 25 – 1	Aug. 22 – 0	Aug. 20 – 0	Aug. 5 – 0
Aug. 28 – 3	Aug. 24 – 0	Aug. 23 – 4	Aug. 6 – 3
Aug. 31 – 10	Aug. 31 – 113	Aug. 24 – 0	Aug. 11 – 0
		Aug. 25 – 0	Aug. 12 – 0
		Aug. 28 – 0	Aug. 14 – 0
Sept. 1 – 0	Sept. 8 – 181		
Sept. 7 – 0	Sept. 12 – 216		
Sept. 14 – 0	Sept. 16 – 7		

* The three exposures on August 12 were of 5 minutes duration and were made by three different patrols at altitudes of 3,000, 4,000, and 5,000 feet, respectively.

Vertical Distribution of Spores. As rust spores are readily air-borne, it is apparent that upward air currents might carry them to relatively high altitudes. On the patrol flights referred to above, most of the exposures were made at altitudes between 1,000 and 5,000 feet. Within this range, spores did not appear to be more numerous at one altitude than at another.

In order to ascertain the relative concentration of spores in the atmosphere at successively higher altitudes, a series of special flights was made in Manitoba at Portage la Prairie in 1930 and at Winnipeg in 1931. The data are recorded in Table 5. In these flights the pilot made an exposure at the lowest altitude, then rose to the next higher one and made the second exposure, and so on until the highest and last exposure of that series was made. The space of time between the first and last exposure was, therefore, relatively short. In connection with Table 5, it should be recalled that during late July and in August, 1930, a moderate to heavy outbreak of stem rust was present in Manitoba, while in 1931 there was but a light infection. In the latter year, cereal crops ripened early and harvesting operations were well under way by the first week of August.

It would appear from Table 5 that, on those days in which several thousand spores were intercepted by the slides, the concentration of spores was greatest up to 5,000 feet or thereabout. This is evident from the exposures made in late July and in the first half of August. There is no way of determining where these spores originated, but presumably a large proportion of them were produced in Manitoba. The exposures made in June and the first three weeks of July, 1931, show that the distribution of spores in the air was rather uniform to considerable heights during that period, a fact which suggests that the spores had travelled a considerable distance and had become more or less uniformly distributed through the atmosphere.

TABLE 5.—THE NUMBER OF STEM-RUST SPORES PER SQUARE INCH INTERCEPTED BY MICROSCOPE SLIDES EXPOSED AT DIFFERENT ALTITUDES FOR 10 MINUTES ON EACH OF SEVERAL DIFFERENT DATES IN 1930 AND 1931

Date	Number of spores at different altitudes					
	1,000 ft.	3,000 ft.	5,000 ft.	7,000 ft.	10,000 ft.	14,000 ft.
1930						
July 29	756	—	684	—	2	6
Aug. 1	13,920	—	1,440	—	7	16
Aug. 5	24,200	—	7,560	—	108	10
Aug. 8	1,596	—	30	—	21	18
Aug. 12	4,200	—	9	—	19	12
Aug. 13	6,096	—	48	—	21	5
Aug. 14	24,000	—	170	—	36	30
1931						
June 15	1	0	0	0	0	5
June 22	1	1	1	3	3	4
June 29	1	0	1	1	1	2
July 7	3	1	1	0	0	0
July 13	4	4	0	1	1	2
July 20	4	2	0	0	0	1
July 27	6,840	8,760	6,360	1	1	0
Aug. 5	3,685	1,800	9	0	No exposure	No exposure

Horizontal Distribution of Spores. Not much information concerning the horizontal distribution of spores was obtained through the aeroplane-slide exposures, but the few data bearing on this point are in agreement with those of the stationary-slide exposures. From the latter exposures (Table 2), it is abundantly clear that the concentration of stem-rust spores in the atmosphere near ground level varies greatly from place to place and from time to time. The data furnished by the aeroplane exposures, although relatively few, indicate that, at an altitude of approximately 5,000 feet, the horizontal distribution of spores is by no means uniform. For instance, on September 15, 1926, at Lac du Bonnet, which is situated at the southern extremity of Lake Winnipeg, a 5-minute exposure was made at 5,000 feet on each of three different patrol routes. The exposure on one route intercepted ninety times as many spores as either of the exposures on the other two routes. Within the same general region, there was, therefore, a pronounced difference in the number of spores. On July 11, 1929, an exposure at Lac du Bonnet collected three times as many spores as one at Portage la Prairie, 110 miles distant. The reverse result was obtained on July 29, 1930, from two exposures made at Portage la Prairie and one at Lac du Bonnet. At approximately the same altitude, the concentration of spores at Portage la Prairie was nearly one hundred times that at Lac du Bonnet.

PLACE OF ORIGIN OF EARLY WIND-BORNE INOCULUM

If, as is evident from the foregoing discussion, wind-borne inoculum is responsible each year for the initiation of stem rust in Western Canada, the question naturally arises as to where this inoculum originates. Obviously it must originate in an area where the growing season is somewhat earlier than in Western Canada, for, in an area with a later growing season, climatic conditions would undoubtedly prevent stem rust from developing until a correspondingly later date, and hence inoculum would not be available for dissemination. Not only must inoculum be present in the area, but it would seem necessary that it be present in considerable abundance before it could be effectively disseminated long distances. Furthermore, in order that inoculum be introduced into Western Canada, there must be during June and July one or more periods in which the wind is favourable to the introduction of inoculum from whatever area is in question. These restrictive qualifications would seem to limit very largely the area of inoculum origin to the Mississippi Valley.

The first two qualifications would seem to eliminate to a great extent the Pacific Northwestern States and British Columbia as areas of inoculum origin. In the Pacific Northwestern States, a considerable acreage is sown to cereals, but the growing season is usually concurrent with or somewhat later than that of the Upper Mississippi Valley, and hence the former area has no advantage over the latter in respect to earliness of stem-rust development. Furthermore, in the Inland Empire, a large agricultural region lying between the Rocky and the Cascade Mountains, stem rust is rarely of economic importance (85), although it is frequently severe, apparently, in other parts of these States (67). In British Columbia, the cereal acreage is small; the growing season is still later; and stem rust is usually of minor importance, except occasionally in a few localities.

Then, too, the presence of high mountain ranges, running in a general north-to-south direction in both these areas, would tend to interpose a considerable barrier to the spread of inoculum across these ranges, although probably not an insuperable barrier. As is pointed out later, there is a probability that, when inoculum is available in these areas, it can be brought by winds into Western Canada. It is, however, improbable that the early inoculum reaching Western Canada, or indeed in most years, any considerable amount of later inoculum originates in these two areas.

On account of the lateness of the growing season and the scarcity of susceptible grass hosts in the territory lying north of the cultivated area of Western Canada, there is practically no possibility that whatever slight amount of inoculum arises there can be produced early enough to influence in any way the course of the disease in the cultivated area.

As far as Ontario is concerned, the territory lying north of Lake Superior and Lake Huron and extending from Manitoba to the western boundary of Quebec is developed comparatively little agriculturally, and throughout this territory the growing season is later than in Western Canada. Whatever inoculum may develop there is produced too late to initiate early infections and too small in quantity to influence appreciably the amount of infection in Western Canada, even if it did reach this area. The only part of Ontario in which inoculum for early dissemination could arise is the area lying immediately north of Lake Erie and Lake Ontario. in this area, local outbreaks of stem rust originating from infected barberry frequently occur, and in occasional years general outbreaks develop, but it is unlikely that inoculum is ever produced there in sufficient abundance to provide early inoculum for Western Canada. Moreover, as is pointed out later, the occasions on which either early or later inoculum from this area could be carried by winds into Western Canada are extremely rare, if indeed such occasions occur.

The probability of inoculum produced in such eastern States as New York, Pennsylvania, and Ohio, reaching Western Canada seems to be just about as small as it is of inoculum produced in southern Ontario. Still less is the probability of inoculum produced in Quebec and the Maritime Provinces, or the New England States being carried by winds to Western Canada. There is a better possibility of inoculum being carried in from Wisconsin, Illinois, and Michigan, but the most probable source of the early inoculum, as well as of the later arriving inoculum, is the western Mississippi Valley, particularly the more northerly part of it.

As is well known, the Mississippi Valley comprises a vast cereal-growing area, extending from the Gulf of Mexico to the Canadian border, and immediately adjoining Manitoba and eastern Saskatchewan. In it, crops ripen successively later from south to north, so that with favourable weather conditions it would be possible in one season for stem rust to spread from south to north throughout its full length. As mentioned earlier, stem rust overwinters practically every year to a greater or less extent in the extreme south, in the State of Texas, and in some years at least there is definite evidence of the spread of stem-rust spores from southern to northern States (67, 94, 113, 156, 157, 158, 192, 193, 195, 198, 209, 226). This progressive advance has been observed in the field in such years as 1904 (67, 85), 1935 (195), 1937 (199), and 1938 (140). Further-

more, in the northern States, barberry becomes infected every year, so that even in a year when there may be little or no northward drift of spores from the south, inoculum may spread from infected barberries (57, 102, 141, 144, 149, 169, 189, 191, 192, 205) to cereal crops in this area, and inoculum produced on these crops may then spread northward into Western Canada. It may be mentioned here, however, that owing to the extensive eradication of the common barberry in the northern States, this source of infection is continually becoming of less importance (94, 156, 157, 195, 211) for both areas.

In the present investigation, definite evidence of northward spread of inoculum from the Mississippi Valley into Western Canada has been obtained, but as this evidence can be more conveniently presented in connection with the discussion on the relation of wind to the spread of stem rust, it is reserved for that section of this paper. The inoculum arriving in Western Canada in June and early July apparently may come from as far south as southern Iowa, or possibly even from farther south, but the bulk of the later arriving inoculum probably originates in the more northerly States of the Mississippi Valley. A comparison of the severity of the stem-rust outbreaks in the northern Mississippi Valley and Western Canada over a period of years and of the predominating physiologic races of the rust present in different years in the two areas, seems to support the conclusion that outbreaks in Western Canada are largely northward extensions of outbreaks in the northern Mississippi Valley.

Comparison of Stem Rust Severity in the Upper Mississippi Valley and Western Canada

From the fact that Western Canada lies immediately north of the Mississippi Valley, it can readily be understood that the amount of stem-rust infection in the more northerly portion of the latter area, namely the Upper Mississippi Valley, may have a very direct influence on the amount of infection that develops in Western Canada. If allowance be made for differences in latitude, climatic conditions in the two areas are not greatly dissimilar. Moreover, the topography of the two areas is much alike. There is also a good deal of similarity in the varieties of small grains grown. As no natural barriers separate the two areas, south winds can readily carry spores from the one into the other. It would not, therefore, be surprising to find considerable agreement from year to year in the intensity of infection in the two areas.

Table 6 gives the years, from 1904 to 1938, in which stem rust was of heavy, medium, and light intensity in the Upper Mississippi Valley and Western Canada. The classification of the years from 1904 to 1925 for the former area is that given by Stakman and Lambert (207) and Lambert (113), while that of the years from 1926 to 1938 is based on reports in the *Plant Disease Reporter* and its Supplements[8] for those years.

As shown in Table 6, there is a good deal of agreement year by year in the severity of stem rust in the Upper Mississippi Valley and in Western Canada, although some divergencies are evident. The agreement, however,

[8] Mimeographed publications of the United States Department of Agriculture.

may be somewhat closer than represented, for in some instances it was difficult to decide whether or not a particular year should be classified more properly as a heavy rust year rather than as a medium rust year, or as a medium rust year rather than as a light rust year. Where the difficulty could not be satisfactorily resolved, the class representing the lesser rust severity was chosen. For example, in 1911 stem rust is known to have been at least rather heavy in southern and central Manitoba and prevalent in south-eastern Saskatchewan, but whether or not epidemic conditions prevailed is uncertain and hence, for Western Canada, 1911 is classed as a medium rust year rather than as a heavy rust year, although if more exact information had been available it might have been more accurately classed as a heavy rust year, and thus be brought into agreement with the classification given it in the Upper Mississippi Valley. The year 1919 could be classed with some justification as a heavy rust year, but it seems more in keeping with the actual conditions that prevailed to regard it as a medium rust year. The greatest disparity in the severity of infection in the two areas seems to have occurred in 1920, but although this year is classed as a light rust year in Western Canada, it would probably have been almost as correct to have regarded it as a medium rust year. In some other years, stem rust was somewhat heavier in one area than in the other, but probably in no year has the difference in the in tensity of infection in the two areas been greater than that which could be justifiably attributed to local differences in weather conditions. The comparison, therefore, shows that during the period 1904 to 1938 there was agreement in the amount of stem rust in the two areas in 26, and apparently in more, of the 35 years, a fact that leaves little doubt that the amount of infection in the northern Mississippi Valley has a direct influence on the amount that develops in Western Canada.

TABLE 6.—CLASSIFICATION OF THE YEARS FROM 1904 TO 1938 ACCORDING TO THE INTENSITY OF STEM-RUST INFECTION IN THE UPPER MISSISSIPPI VALLEY AND WESTERN CANADA

Class of year	Upper Mississippi Valley	Western Canada
Heavy rust	1904, 1911, 1916, 1919, 1920, 1923, 1927, 1935, 1938.	1904, 1916, 1923, 1927, 1935, 1938.
Medium rust	1905, 1906, 1908, 1914, 1917, 1921, 1922, 1925, 1929, 1937.	1905, 1906, 1911, 1914, 1919, 1921, 1924*, 1925, 1930, 1937.
Light rust	1907, 1909, 1910, 1912, 1913, 1915, 1918, 1924, 1926, 1928, 1930, 1931, 1932, 1933, 1934, 1936.	1907, 1908, 1909, 1910, 1912, 1913, 1915, 1917, 1918, 1920, 1922, 1926, 1928, 1929, 1931, 1932, 1933, 1934, 1936.

* A light rust year except in Manitoba.

Comparative Prevalence of Physiologic Races of Wheat Stem Rust in the United States and Canada

As wheat stem rust comprises a large number of different physiologic races, it would be expected that if infection in Western Canada is initiated by wind-borne spores from the south there should be an evident agreement in the identity and prevalence of at least the predominating races found in Western Canada and in the northern Mississippi Valley. Unfortunately, data for the latter area are only available for the four years discussed below, but for a few of the other years some idea of the prevalence of the different races in the two areas can be obtained by a comparison of what data are available for the United States as a whole with corresponding data for all of Canada, as the predominating races in the two areas under consideration appear to be the predominating ones in the two countries.

Stakman, Levine, and Wallace (209) made a study of the distribution and prevalence of the physiologic races of stem rust present in the Mississippi Valley in 1926, 1927, and 1928, with a view to determining whether or not such a study would provide evidence of the spread of inoculum from southern to northern States. Wallace (226) extended the study to include the whole of the United States, and with data obtained by Canadian workers made comparisons of the relative prevalence of the races of stem rust present in the United States and Canada in 1926 and 1927. (Complete data for Canada in 1928 were not available at the time that he made the comparison.) He found that, in 1926, ten of the 15 races obtained in Canada were present in the United States, the other 5 races comprising only 9 out of a total of 387 isolates. In 1927, eleven of the 19 races obtained in Canada were present in the United States. The other 8 races comprised 30 out of a total of 511 isolates. Two of these 8 races (Races 56 and 57) were obtained from infected barberry plants in the greenhouse at Winnipeg, and another (Race 53) originated at Ottawa in the vicinity of barberry. Actually, therefore, in 1927 only 5 races were found, apart from barberry, on cereals and grasses in Canada that were not found in the United States. Wallace points out that 2 or 3 races were moderately prevalent in Canada but were not found, or were found only rarely, in the United States in these years.

The comparison begun by Wallace can now be completed for 1928, and extended to include 1939, a year for which complete data are available (210). In 1928, nineteen physiologic races were found in the United States. Twelve of these races were also found in Canada, but, in addition, there were 9 others found in Canada that were not found in the United States. Six of these 9 were collected in Eastern Canada, and may have had their origin on infected barberry. In 1939, fourteen races were identified in the United States, 7 of which were found present in Canada. Nine other races were collected in Canada, although 6 of them were only soliated once.

Table 7 gives the comparative prevalence of the more commonly occurring races in the United States and in Canada during the years 1926, 1927, 1928, and 1939, and of the same races in 9 (8 in 1939) States in the Mississippi Valley—Iowa, Kansas, Minnesota, Missouri, Montana, Nebraska, North Dakota, South Dakota, Wisconsin—and in Western Canada during the same years.

TABLE 7.—PREVALENCE OF THE MORE COMMONLY OCCURRING PHYSIOLOGIC RACES OF STEM RUST IN THE UNITED STATES AND CANADA, AND IN NINE STATES OF THE MISSISSIPPI VALLEY AND IN WESTERN CANADA, IN 1926, 1927, 1928, AND 1939, EXPRESSED AS THE PERCENTAGE THAT THE ISOLATES OF EACH RACE FORMED OF THE ISOLATES OF ALL RACES IDENTIFIED IN THE RESPECTIVE YEARS AND COUNTRIES OR AREAS

Physiologic race	1926		1927		1928		1939	
	United States	Canada	United States	Canada	United States	Canada	United States	Canada
11*	17.2	3.2	7.6	0.9	6.2	1.3	3.2	1.9
14	0.9	0.5	0.7	3.5	0.0	0.5	0.1	0.6
15	0.0	0.5	0.0	1.8	0.0	5.4	0.3	0.6
17*	8.6	7.7	4.2	4.2	3.8	4.3	10.0	2.6
19	0.9	0.3	2.0	0.2	2.9	1.5	3.3	3.2
21	10.3	22.3	29.3	29.5	19.2	26.3	0.4	0.0
34	0.9	1.1	0.0	2.2	0.3	3.8	0.6	0.0
36*	56.0	55.7	37.6	45.3	30.7	39.3	0.7	0.6
38*	7.7	4.8	12.5	5.8	25.4	8.2	24.0	11.5
49	0.0	0.8	2.2	1.8	7.1	3.6	0.6	0.0
56	0.0	0.0	0.0	0.0	0.6	0.0	55.5	74.3
Total number of isolates	116	378	406	450	339	391	1063	156
	Nine States	Western Canada	Nine States	Western Canada	Nine States	Western Canada	Eight States†	Western Canada
11*	7.0	2.2	5.7	0.5	5.6	0.9	2.7	1.9
14	0.0	0.4	0.4	3.8	0.0	0.3	0.2	1.0
15	0.0	0.7	0.0	2.0	0.0	5.1	0.2	0.0
17*	1.7	7.4	4.8	4.3	4.7	4.8	12.3	1.9
19	0.0	0.4	2.2	0.0	2.3	1.6	2.9	3.9
21	10.5	22.6	31.3	30.1	24.7	29.6	0.3	0.0
34	1.7	1.1	0.0	2.3	0.5	3.5	0.5	0.0
36*	71.7	60.5	43.6	47.2	39.6	44.2	0.6	0.0
38*	1.7	0.4	6.5	3.3	12.6	2.9	19.0	9.6
49	0.0	0.7	2.6	1.8	6.5	3.5	0.5	0.0
56	0.0	0.0	0.0	0.0	0.9	0.0	60.5	76.9
Total number of isolates	57	269	229	391	219	314	625	104

* Races 11, 17, 36, and 38 differ only slightly from Races 32, 29, 18, and 39, respectively, and under some conditions are almost or wholly indistinguishable from them. For purposes of the present computation, it seems advisable to regard each pair of races (e.g. Races 11 and 32) as a single race. The percentages, therefore, given for Races 11, 17, 36, and 38 in this table include those also, respectively, of Races 32, 29, 18, and 39.
† No data given for Montana in this year.

In this table, the prevalence of a particular race in a given year is expressed as the percentage that the isolates of this race formed of the total of all the isolates obtained in that year in the respective country or area. It may be mentioned in passing that few of the isolates obtained in the United States in these years originated on infected barberry, and none of

those obtained in Canada from infected barberry are included in the table. The most arresting feature of the data is the pronounced dominance in both countries, or in both regions, of a few physiologic races, namely Races 21, 36, and 38 from 1926 to 1928, and of Races 38 and 56 in 1939. Race 38 was apparently less prevalent in the nine States and in Western Canada during the period 1926-1928 than in other parts of the two countries. In all four years, Races 11 and 17 were present in both countries, although Race 11 tended to be considerably more prevalent in the United States than in Canada, while Race 17 tended to be about as prevalent in the one as in the other. The other races were in most instances less prevalent than those just mentioned, and were more often than not present in both countries.

It is obvious that, according to Table 7, there were certain disparities in the prevalence of some of the races, at least in some years, in the two countries, and even in the Mississippi Valley and Western Canada. For example, Race 15 was not isolated in 1926, 1927, or 1928 in the United States, although it was isolated in Canada in all three years and apparently was not altogether uncommon there in the last two of these years. Similarly, Race 34 was not isolated in the United States in 1927, although, in that year, it was isolated 10 times in Canada from collections of stem rust obtained from cereals and grasses. In this connection, it may be remarked that the fact that, in one or more years, a given race was found present in Canada but not in the United States does not necessarily indicate conclusively that the race was entirely absent from the latter country. The converse is likewise true. On the other hand, the presence of Race 15 in Canada for three consecutive years and the failure in the United States to isolate this race in the same years, might indicate that the race overwintered in Western Canada. It would seem almost a mathematical certainty that Race 15 was not present in the Mississippi Valley in 1927 and 1928. Whatever may be the explanation of such anomalies, they in no way impair the strength of the positive evidence, and as adequate discussion of them would be long and probably tedious, they need be given no further consideration. The fundamental point made evident by the comparisons given in Table 7 is the pronounced similarities in the racial composition and prevalence of the rust in the areas under discussion. The fact that in each year the races predominating in the northern Mississippi Valley were the races that predominated in Western Canada, can leave little doubt as to the main source of the inoculum responsible for stem-rust outbreaks in the latter area.

For the decade following 1928, as already mentioned, detailed data relative to the prevalence of different races of stem rust in the United States are not available for comparison, except in the case of Race 56, which will be referred to presently; but Stakman and coworkers (201, 204) point out that in the United States as a whole there have been decided population drifts among physiologic races of wheat stem rust between 1930 and 1939. Similar trends in the prevalence of races of this rust have been observed in Canada (146) during these and earlier years. The data available for the United States are only illustrative and hence not extensive, but they furnish at least a limited basis for comparison. In this comparison, as in the foregoing one, the prevalence of a race in a given year is

expressed as the percentage that the isolates of the race in question formed of the total isolates of all the races found in that year in each country. The corresponding data for the two countries in the period just indicated are as follows:

—	United States	Canada
Race 21	7% in 1934, not found on wheat in 1939.	13.7% in 1934, not found on cereal or grasses in 1938 or 1939.
Race 34	0.6% in 1930, 22% in 1934, 0.6% in 1939.	7.3% in 1930 (1.3% in 1929), 19.2% in 1934, 0.0% in 1939 (1.7% in 1938).
Race 36*	36% in 1930, 0.6% in 1939.	49% in 1930, 4% in 1939.
Face 38*	Fluctuated greatly, 34% in 1930, 4% in 1934.	Fluctuated widely, 20.3% in 1930, 2.7% in 1934.
Races 17* and 19	Tended to increase slowly but irregularly.	Fluctuated considerably, but definite tendency to increase only evident in Race 17.

* See first footnote to Table 7.

From these few comparative data, it is evident that there is a parallelism between the population trends of at least certain of the more prevalent physiologic races of wheat stem rust in the two countries, although there is some disparity in the relative prevalence of individual races.

A better sequence of data is available for Race 56. In 1928, this race comprised 0.59%, and, in 1930 comprised 0.3% of all isolates made in the United States, but it was not collected on cereals or grasses in Canada until 1931, when it comprised 2.0% of all the isolates. From 1932 to 1938, the yearly prevalence of this race in the United States and Canada is indicated by the following percentages:

—	1932	1933	1934	1935	1936	1937	1938
	%	%	%	%	%	%	%
United States	2.1	3.7	33.1	44.0	47.0	57.0	66.0
Canada	7.7	5.7	28.8	50.0	61.0	53.3	69.4

The gradual increase year by year in the prevalence of this race from 1933 to 1938 in both countries is a striking feature of the rise to prominence of Race 56, and leaves little doubt that the prevalence of this race in the United States has been largely responsible for its prevalence in Canada.

Although the comparative data presented above relative to the prevalence of physiologic races of wheat stem rust in the United States and in Canada are somewhat fragmentary, the general trend of the evidence indicates that in any given year the races most prevalent in the United States are the races most prevalent in Canada, and that population trends among these races tend to correspond in the two countries. As stem rust develops earlier in the United States than in Canada, the conclusion seems justified that inoculum from the United States is introduced into Canada, the predominating races in the former providing the bulk of the inoculum and thereby becoming estalbished as the predominating races in the latter.

RELATION OF METEOROLOGICAL FACTORS TO THE DEVELOPMENT OF STEM RUST

The influence of such meteorological factors as humidity, temperature, and light intensity on the development of stem rust has been carefully studied under controlled conditions by different investigators, and some attention has been given to wind as a means of spore dispersal. Many observations have been recorded of the relation of these factors, particularly temperature and humidity, to stem-rust development under natural conditions. In regard to this relation, it may be mentioned that it is complicated by the complex life cycle of the organism (Figure 6) and by the fact that the organism, except in the case of free spores, cannot be studied apart

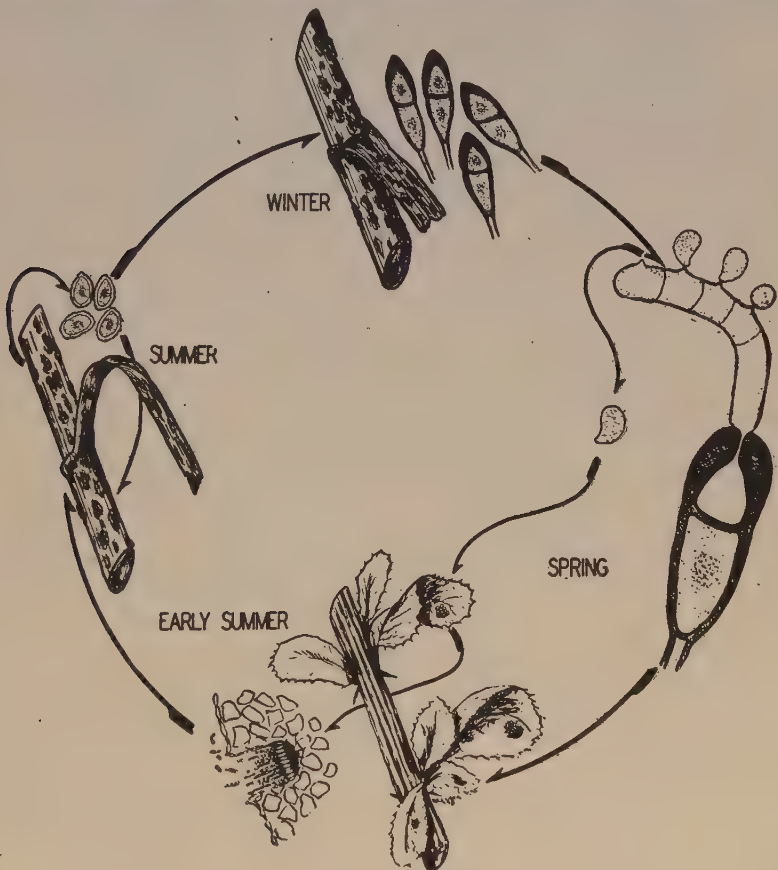

FIGURE 6. Schematic representation of the life cycle of the stem-rust fungus. The black spores (teliospores) survive the winter and germinate in the spring and early summer. Each of the 2 cells of a black spore produces a stout curved tube on which are produced 4 tiny colourless spores (sporidia), which infect common barberry. Infections on barberry produce the cluster-cup stage of the fungus. The cluster cups (aecia) produce aeciospores, and these spores infect cereals and grasses. Infections arising from them produce the red, or summer, spores. These spores (Figure 7), in turn, infect cereals and grasses; and so long as the plants remain green and weather conditions are favourable, old and new infections continue to produce urediospores, and the urediospores, new infections. When, however, the plants begin to ripen, the infections cease to produce urediospores but, in their place produce the black spores (teliospores), thus completing the life cycle of the fungus. (Drawing by Mr. W. E. Clark).

from its hosts. In the present study, however, it is only necessary to consider weather conditions in their relation to the uredial stage of the fungus, for it is with this stage (Figure 7) that the present study is almost

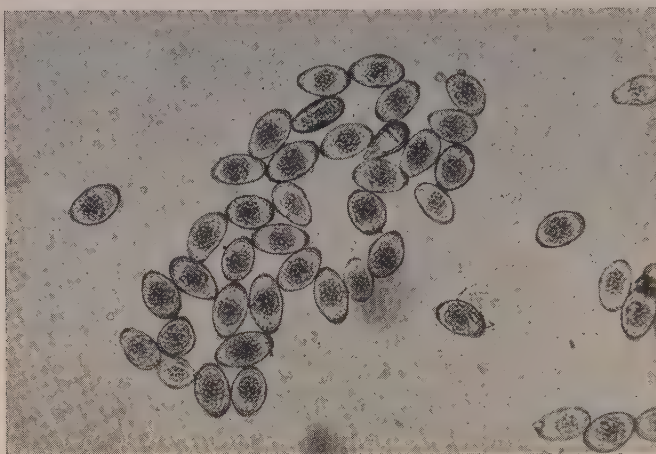

FIGURE 7. Red spores (urediospores) of stem rust. Magnification, 230 app.

entirely concerned. For a discussion of the relation of weather conditions to the other stages, and for literature citations bearing on the same, the reader is referred to Lambert (113), Zimmerman (239), and Lehmann, Kummer, and Dannenmann (117).

As earlier pointed out, there are great variations in the severity of stem-rust infection in Western Canada from year to year. In any given year, the severity is usually greatest in eastern Manitoba and decreases westward to Alberta. In order to ascertain to what extent these yearly and regional variations in rust severity are attributable to weather conditions, a study has been made of certain meteorological factors for the years 1916 to 1938, and of the relation of these factors to the development of stem rust in these years.

Because of regional differences in climatic conditions in Western Canada, the Meteorological Service of Canada recognizes a number of meteorological divisions in this area. The divisions included in this study are as follows:

Manitoba:	Red River (Eastern Manitoba).
	Qu'Appelle and Assiniboine Rivers (Western Manitoba).
Saskatchewan:	Qu'Appelle River (Eastern Saskatchewan).
	Saskatchewan Forks (North-central Saskatchewan).
	North Saskatchewan River (North-western Saskatchewan).
	South Saskatchewan River (South-western Saskatchewan).
Alberta:	North Saskatchewan River (Northern Alberta).
	Red Deer River (Central Alberta).
	Bow River (Southern Alberta).

These nine divisions embrace the greater part of the cultivated area of Western Canada. The two Manitoba divisions and the Qu'Appelle division in Saskatchewan comprise approximately the area most affected by stem rust. The meteorological data are presented mainly by meteoro-

logical divisions, for the reason that, if the severity of rust infection in these divisions is closely associated with seasonal weather conditions, this arrangement of the data would seem best suited to establish the association.

For purposes of this study, the years of the period just mentioned are divided (as shown in Table 6) into three classes, namely, light, medium, and heavy rust years, depending on the severity of the infection in the different years. Owing to variations in the intensity of the infection present in different meteorological divisions in individual years, these class designations relate to individual divisions rather than to Western Canada as a whole. Table 8 indicates the relative intensity of stem-rust infection in the different meteorological divisions for years in which stem-rust infection was moderate or severe in any one of the divisions. The other years of the period under discussion are regarded as light rust years in all the meteorological divisions.

The meteorological factors considered are humidity, temperature, light, and wind. In order to conserve space, data for individual years are not presented, except where imperative. For the same reason, the data relative to wind are largely restricted to the Red River division in Manitoba, where the relation of wind to stem-rust development is most clearly demonstrable. The data on light (hours of sunshine) and on relative humidity are given for certain stations, which may be regarded as representing the divisions in which they are situated. Owing to marked yearly differences, during the growing season, in the amount and frequency of rainfall in different parts of each division, and to rather wide fluctuations in temperature from day to day, and even in a single day, it is virtually impossible closely to relate such differences and fluctuations to the general development of stem rust in any given year. Perhaps the best that can be done is to determine if, in the different divisions during the period under review, the averages of the meteorological data for the medium and the heavy rust years show an appreciable deviation from those for the light rust years and for the whole period. Therefore, the data are given, wherever possible, as averages for each class of years.

TABLE 8.—SEVERITY OF STEM-RUST INFECTION ON WHEAT, BY METEOROLOGICAL DIVISIONS, IN MANITOBA, SASKATCHEWAN, AND ALBERTA IN MEDIUM AND HEAVY RUST YEARS BETWEEN 1916 AND 1938

Year	Manitoba		Saskatchewan				Alberta		
	Red River	Qu'Appelle and Assiniboine Rivers	Qu'Appelle River	Saskatchewan Forks	North Saskatchewan River	South Saskatchewan River	North Saskatchewan River	Red Deer River	Bow River
1916	H*	H	H	M	L	L	L	L	L
1919	M	M	M	M	M	L	L	L	L
1921	M	M	M	M	M	L	L	L	L
1923	H	H	H	M	L	M	L	M	M
1924	M	M	L	L	L	L	L	L	L
1925	M	M	M	M	L	L	L	L	L
1927	H	H	H	M	M	L	M	M	L
1930	M	M	M	L	L	L	L	L	L
1935	H	H	H	M	L	L	L	L	L
1937	M	M	L	L	L	L	L	L	L
1938	H	H	H	M	M	M	M	M	M

* Signification of symbols: H = Heavy infection, M = Medium infection, L = Light infection.

Relation of Humidity to Stem-Rust Development

Spore germination and infection are the initial stages in the establishment of stem-rust infection, and these two processes cannot take place except in the presence of a sufficiency of moisture. The humidity range for germination and infection, unlike the temperature range, is very narrow indeed. Beauverie (13) states that urediospores of stem rust require to be in contact with liquid water before they will germinate. Stock (214) obtained no germination at 90, 95, or 99% relative humidity, and very little germination at 100% when no condensation water was present on the spores; but abundant germination occurred at 100% humidity when a thin film of moisture collected around them. On the other hand, Lauritzen (115) obtained some infection on inoculated plants kept at a relative humidity of 95%. Regarding this result, it may be pointed out that unless the temperature is kept constant there is the possibility that a slight temporary drop in temperature may cause the deposition of water droplets around the spores, in which case the spores may germinate not in a moist atmosphere but actually in water. As a matter of fact, in high air humidities, it is difficult to prevent such condensation droplets from forming.

The likelihood is that under field conditions stem-rust urediospores only germinate when there is liquid water present on the plants. To secure abundant infection, this condition must persist for a considerable number of hours. On seedling plants freshly inoculated and placed in moist chambers, Stakman and Levine (208) obtained the best infection on plants held in the chambers for 48 hours. Gassner and Straib (76) secured maximum infection on plants kept in moist chambers for 18 hours at a temperature of 62.6°-68° F., but recommend that the period should usually be 48 hours. Some infections, however, may occur within a much shorter period. Peltier (154) inoculated a series of seedling plants and placed them in moist chambers for different periods of time. Infection developed subsequently on 1.7% of those kept in the chambers for from 3 to 5 hours, on 17% of those kept for 6 hours, on 78% of those kept for 22 hours, and on 100% of those kept in the chambers for 36 hours. It would appear, therefore, that moisture must be present on the plants for at least a few hours to insure that infection, however slight, may be established.

Amount of Rainfall

The opinion is very widely held that wet seasons are usually seasons of heavy stem-rust infection, and this opinion is supported by numerous observations made over a long period of time. Eriksson and Henning (59) review the observations made up to 1896 and conclude from these and their own observations that the development of stem rust is favoured by abundant rainfall in July and early August, as, at that time of year in the areas under review, urediospores are most numerous and readily germinable. Sorauer (188), in 1909, enumerates some of the observations made during the preceding two decades on the relation of rainfall to stem-rust outbreaks. In general these observations indicate an association between periods of wet weather and severe attacks of stem rust. This association between wet seasons and heavy rust has been very frequently observed (9, 13, 14, 17, 25, 34, 37, 47, 143, 172, 199, 215, 222, 227). Freeman and

Johnson (67) point out that in the United States although cereal rusts are practically coextensive with their hosts, they are generally only a menace to cereal crops in areas with an annual rainfall of 20 or more inches. Levine (118) found that 90 to 100% infection of stem rust on wheat occurred at stations only where the precipitation exceeded 2.5 inches during the last two months of wheat development.

On the other hand, it is generally recognized that drenching rains tend to wash off the spores from the plants and thus limit the number of infections. According to Eriksson and Henning (59) this observation was made by Nielsen in 1874, and subsequently by Wold and by Sorauer. Bolley (23), Klebahn (111), Freeman and Johnson (67), and Stakman (189) made the same observation. Bolley points out that rain by day is of little consequence for infection unless the rain is light and the weather cloudy. Klebahn remarks that it is the humid atmosphere after rain that favours infection and that this condition can be brought about better by drizzling rain than by heavy showers. Roussakov (170) regards long continued light rain as more conducive to rust development than heavy showers, and rain at night more so than rain by day. He is of the opinion that rust development is not so much dependent on the total amount of rain as on the duration and frequency of the rains.

That rust infestation is not always severest in seasons of highest rainfall is shown by Freeman and Johnson (67) in a study of weather conditions during the 3-year period 1903-05 in the Mississippi Valley. In this area, stem-rust infection was of moderate intensity in 1903, somewhat heavier in 1905, and extremely severe in 1904. An analysis of the precipitation data showed that the year 1905 had a greater rainfall than either 1903 or 1904, whether the period studied covered the seven months or the three months prior to harvest, or the month in which the grain headed. During the three months preceding harvest, the rainfall in 1904 was below normal in all but 3 of the 10 States embraced in the study, namely, in Kansas, Missouri, and North Dakota. Furthermore, Gassner (71) relates that, in Uruguay, there is no relation between the amount of rain and the amount of stem-rust infection. Zekl (238) states that seasons of heavy infection have low precipitation but high atmospheric humidity. Lambert (113) concludes from a comprehensive study of the relation of humidity to stem-rust development in the Upper Mississippi Valley that differences in the total precipitation during May, June, and July did not seem to be associated in any way with the development of stem-rust epidemics. He remarks that "severe epidemics sometimes develop in parts of the Red River Valley in which rainfall is totally absent" while the attack is developing.

Rainfall in Western Canada. The belief is very commonly held by farmers and others in Western Canada that there is a close association between wet seasons and heavy outbreaks of stem rust. This association was mentioned by Bedford (17) in 1903 and again by Bracken (25) in connection with the 1916 epidemic. In order to determine to what extent seasonal rainfall is associated with outbreaks of stem rust, rainfall data for the nine meteorological divisions earlier mentioned have been assembled for the spring and summer months from 1916 to 1938, and are presented in Tables 9, 10, and 11. The data for the months of April and May are

combined in Table 11, as the rainfall of these two months does not directly influence the development of stem rust, the disease being not then present. The amount of rainfall in these two months, however, influences crop growth and thus indirectly stem-rust development.

Table 9 gives the means of the rainfall for the 5-month period April to August and for the 3-month period June to August in the nine meteorological divisions earlier mentioned. This table shows that in each of the divisions the average rainfall for the 5-month period, as well as for the 3-month period, is greater both in the medium and in the heavy rust years than in the light rust years, and hence the respective means for the whole period of years occupy in each division an intermediate position between the medium and heavy rust years and the light rust years. There is, therefore, a distinct tendency in Western Canada for years of medium or heavy rust infection to be associated with years of above-average spring and summer rainfall.

TABLE 9.—MEAN RAINFALL IN MANITOBA, SASKATCHEWAN, AND ALBERTA, BY METEOROLOGICAL DIVISIONS, FOR THE 5-MONTH PERIOD APRIL TO AUGUST AND FOR THE 3-MONTH PERIOD JUNE TO AUGUST, FROM 1916 TO 1938, FOR YEARS IN WHICH STEM RUST WAS LIGHT, MEDIUM, AND HEAVY IN THE DIVISIONS INDICATED

Meteorological Divisions	Months	Rainfall*			
		Light	Medium	Heavy	23-year period
		in.	in.	in.	in.
Manitoba					
Red River	April – August	9.13	12.52	11.33	10.49
	June – August	6.75	8.68	7.61	7.44
Qu'Appelle and Assiniboine Rivers	April – August	9.61	11.17	13.18	10.80
	June – August	7.11	7.51	9.75	7.79
Saskatchewan					
Qu'Appelle River	April – August	8.07	9.84	11.76	9.18
	June – August	5.77	7.39	8.64	6.67
Saskatchewan Forks	April – August	7.82	10.86	—	8.88
	June – August	5.72	8.11	—	6.54
South Saskatchewan River	April – August	7.63	9.80	—	7.81
	June – August	5.73	7.22	—	5.85
North Saskatchewan River	April – August	8.40	9.60	—	8.61
	June – August	6.30	6.46	—	6.33
Alberta					
Bow River	April – August	8.78	12.20	—	9.08
	June – August	5.61	7.75	—	5.79
Red Deer River	April – August	9.87	12.97	—	10.27
	June – August	6.86	9.18	—	7.12
North Saskatchewan River	April – August	10.13	11.00	—	10.21
	June – August	7.36	7.97	—	7.45

* Amount of rainfall expressed in inches.

On the other hand, it should be pointed out that all heavy rust years were not wet years, or conversely, all wet years, heavy rust years. This fact is evident from Table 10, which gives departures from the normal in the amount of rainfall during the 5-month period April to August and the 3-month period June to August in certain years for five meteorological divisions of Western Canada. The years for which data are given comprise

TABLE 10.—DEPARTURES FROM THE NORMAL IN THE AMOUNT OF RAINFALL FROM APRIL TO AUGUST AND FROM JUNE TO AUGUST IN CERTAIN YEARS BETWEEN 1916 AND 1938 IN FIVE METEOROLOGICAL DIVISIONS OF WESTERN CANADA: MEDIUM AND HEAVY RUST YEARS IN WHICH THE RAINFALL WAS BELOW NORMAL, AND LIGHT RUST YEARS IN WHICH THE RAINFALL WAS ABOVE NORMAL

Meteorological Divisions	Medium and heavy rust years			Light rust years		
	Year	Apr.-Aug.	June-Aug.	Year	Apr.-Aug.	June-Aug.
		in.*	in.		in.	in.
Red River	1916	− 0.24	—	1918	+ 0.51	+ 0.91
	1923	− 2.30	− 1.29	1922	+ 1.31	+ 0.26
	1925	− 0.29	—	1926	—	+ 0.91
	1938	− 1.04	− 1.09	1928	+ 4.96	+ 5.36
Qu'Appelle and Assiniboine Rivers	1919	—	− 0.34	1922	+ 0.70	+ 0.76
	1921	− 0.45	− 1.14	1926	—	+ 0.56
	1924	—	− 0.29	1928	+ 1.20	+ 1.81
	1925	− 0.75	—	1931	—	+ 0.46
	1930	− 0.15	− 0.74	1932	+ 0.70	+ 1.31
	1938	− 2.60	− 1.74	1936	+ 2.35	+ 0.86
Qu'Appelle River	1919	− 0.33	− 0.16	1922	+ 0.70	—
	1925	− 0.53	—	1926	—	+ 0.56
	1930	− 1.78	− 1.37	1928	+ 1.20	+ 1.81
	1938	− 0.93	− 0.64	1931	—	+ 0.46
				1932	+ 0.70	+ 1.31
				1936	+ 2.35	+ 0.86
South Saskatchewan River (Sask.)	1938	− 0.26	− 1.25	1916	+ 6.54	+ 5.65
				1920	+ 0.84	—
				1921	+ 0.84	—
				1922	+ 1.74	+ 1.00
				1924	+ 0.34	+ 0.20
				1925	+ 1.09	—
				1927	+ 5.49	+ 0.75
				1928	+ 1.09	+ 1.85
				1930	—	+ 0.75
				1932	+ 3.24	+ 2.30
				1933	+ 1.19	—
				1935	+ 1.64	—
North Saskatchewan River (Alta.)	1938	− 0.90	− 0.17	1916	+ 3.89	+ 3.35
				1921	+ 0.44	+ 0.25
				1923	+ 3.34	+ 3.65
				1924	+ 0.89	+ 0.90
				1928	—	+ 0.65
				1930	+ 1.09	+ 1.20
				1931	+ 1.39	+ 2.80
				1932	+ 0.44	—
				1935	+ 1.99	+ 1.00
				1937	+ 0.59	+ 0.80

* Departures from normal in amount of rainfall expressed in inches.

TABLE 11.—MEAN MONTHLY RAINFALL IN MANITOBA, SASKATCHEWAN, AND ALBERTA, BY METEOROLOGICAL DIVISIONS, FOR THE MONTHS OF APRIL, MAY, JUNE, JULY, AND AUGUST FROM 1916 TO 1938, FOR YEARS IN WHICH STEM RUST WAS LIGHT, MEDIUM, AND HEAVY IN THE DIVISIONS INDICATED

Meteorological Divisions	April-May			June			July			August		
	Light	Medium	Heavy	Light	Medium	Heavy	Light	Medium	Heavy	Light	Medium	Heavy
	in.*	in.	in.	in.	in.	in.	in.	in.	in.	in.	in.	in.
Manitoba												
Red River	2.30	3.84	3.72	2.70	3.23	2.73	2.28	3.59	2.52	1.78	1.86	2.36
Qu'Appelle and Assiniboine Rivers	2.50	3.66	3.44	2.65	3.28	3.69	2.29	2.40	3.47	2.17	1.83	2.58
Saskatchewan												
Qu'Appelle River	2.30	2.50	3.12	2.43	3.89	3.65	1.62	2.16	3.21	1.71	1.29	1.78
Saskatchewan Forks	2.04	2.71	—	2.49	3.02	—	1.69	2.95	—	1.60	1.82	—
South Saskatchewan River	2.43	2.57	—	2.37	3.90	—	1.81	2.17	—	1.49	1.15	—
North Saskatchewan River	2.10	3.14	—	2.62	1.75	—	1.91	2.85	—	1.77	1.86	—
Alberta												
Bow River	3.18	4.45	—	2.41	3.95	—	1.64	2.27	—	1.54	1.52	—
Red Deer River	3.55	3.78	—	2.48	3.25	—	2.25	3.33	—	2.07	2.90	—
North Saskatchewan River	2.77	3.02	—	2.59	2.45	—	2.60	3.17	—	2.15	2.30	—

* Amount of rainfall expressed in inches.

those medium rust years and those heavy rust years in which the rainfall for the periods indicated was below normal, and those light rust years in which the rainfall for the same periods was above normal. The first three of the divisions for which data are given embrace most of the bad rust area; the other two may be regarded as representing the area relatively free in most years from stem-rust attacks. Table 10 shows that in the Red River division the rainfall for the two periods was definitely below normal in 2 (1923 and 1938) of the 5 epidemic years, and slightly below normal for 1 period (April to August) in 1 other epidemic year (1916) and in 1 medium rust year (1925). In the same division, the rainfall was above normal for the April to June period in 3, and for the June to August period in 4 light rust years. In the second division (Qu'Appelle and Assiniboine Rivers), there was less than normal rainfall for at least one of the periods in 5 medium rust years and in 1 heavy rust year, while there was above-average rainfall for at least one of the periods in 6 light rust years. In the Qu'Appelle River division, 3 medium rust years and 1 heavy rust year had less than normal rainfall in at least one of the periods, whereas 6 light rust years had above-average rainfall.

In the two more westerly divisions (South Saskatchewan River in Saskatchewan and North Saskatchewan River in Alberta), the rainfall in a considerable number of the light rust years was above normal for at least one of the periods. Some of these years are classed as heavy rust years (e.g. 1916, 1923, 1927, and 1935) or as medium rust years (e.g. 1921, 1925, and 1930) in the first three divisions. Attention may be called to the excessive rainfall in both of these westerly divisions in 1916, and in one of them in 1927 and in the other in 1923. The failure of stem rust to reach epidemic proportions in these three years in the westerly divisions of Western Canada was certainly not due to lack of rainfall. If it had been, the Red River division (Manitoba) would be expected to have been comparatively free of stem rust in 1916, for in that year the rainfall in the South Saskatchewan division and in the North Saskatchewan division (Alberta) was, respectively, for the 5-month period 14.35 and 14.10 inches, and for the 3-month period, 11.45 and 10.75 inches, whereas, in the Red River division, where severe infection developed, the rainfall for the 5-month period was 10.25 and for the 3-month period 7.55 inches. Furthermore, stem rust was of medium or severe intensity in 1938 in all of the meteorological divisions, but the rainfall was below normal for both periods in all divisions. Conversely, in 1928, rainfall was above normal for the June to August period and for the April to August period in all divisions excepting the North Saskatchewan division of Saskatchewan, and of Alberta. In some of the divisions, the excess over the normal rainfall was very pronounced in that year, as, for instance, in the Red River division in Manitoba. In spite of the exceptional rainfall, the amount of stem-rust infection was small, in fact about the smallest in any of the years under review. It would appear, therefore, that although an association between years of heavy seasonal rainfall and years of medium and of heavy stem-rust infection does undoubtedly exist in Western Canada, the association is not necessarily a close one and it seems to be dependent on some other factor or factors, chiefly, perhaps, on the abundance of inoculum.

This conclusion is supported by the fact that in 1938 rainfall was below normal in western Saskatchewan and in Alberta, yet stem rust was of medium severity in both these areas. In that year, according to Stakman (197), heavy infection extended unusually far westward in the Mississippi Valley, into Colorado, Wyoming, and Montana. It would seem, therefore, that the widespread occurrence of moderately heavy infection in western Saskatchewan and in Alberta in a comparatively dry year was in no small measure attributable to the introduction of an abundance of inoculum, which introduction was made possible by the unusually far westward extension of heavy stem-rust infection in States to the south and southeast of these two areas. This point will be mentioned again in connection with the discussion of winds favourable to the introduction of spores into different parts of Western Canada.

To ascertain if the higher average rainfall of the medium and the heavy rust years is due to an increased rainfall in any particular month, the rainfall data for the spring and summer months are summarized by months in Table 11 for the same meteorological divisions. In this table, it is seen that the excess of rainfall in the medium and the heavy rust years over the rainfall of the light rust years is spread over the five months. That is to say, the excess is not accounted for by exceptionally heavy rain in some particular month. The average rainfall in April to May and in July in all divisions is higher in the medium and the heavy rust years than in the light rust years; whereas, the average rainfall in June in two divisions, and the average rainfall in August in three divisions, is slightly less in the medium rust years than in the light rust years. It would appear, therefore, that in the medium and the heavy rust years the April to May and the July rainfall was more consistently above average than was the June or the August rainfall.

Frequency of Rainfall

Such terms as damp, humid, moist, rainy, and wet, are commonly used in the literature to describe weather conditions associated with severe outbreaks of stem rust, and there is little doubt that in most cases they imply the frequent occurrence of rain in greater or less amount and of varying duration. Roussakov (170) expresses the opinion that stem-rust development is not so much dependent on the total amount of rainfall as on the duration and frequency of rain, but Klebahn (111) believes that a very high frequency of rain, like heavy rainfall, does not provide the best conditions for the spread of the disease. Tehon and Young (215) show that in Illinois the severe outbreak of stem rust in 1923 was preceded by more than a week of rainy days, and that frequent rains fell during the period in which the disease was becoming established. Peltier (157) states that in most years in Nebraska the lack of an even distribution of sufficient precipitation after primary infection occurs is the major limiting factor in the development of subsequent uredial generations. Tiemann (218) relates that in Silesia heavy showers at intervals occurred during June and July while the heavy attack of 1932 was in process of development. In his study of stem-rust outbreaks in the Upper Mississippi Valley, Lambert (113) finds that during the 22-year period 1904-1925 there was no evident association between years of severe infection and years with a high number of days on which rain in measurable amounts fell.

In the present study, the relation between the occurrence of heavy outbreaks of stem rust and the number of days with rain during the growing season was given consideration. The relevant data are summarized in Tables 12 and 13. Table 12 shows that the average number of days with 0.01 or more inches of rain during the 3-month period June to August in the first three meteorological divisions was upwards of 4 or more days higher in the heavy rust years than in the light rust years, and, in all the divisions, the number is higher in the medium rust years than in the light rust years, although in two divisions the difference is very slight. Table 13 shows that the days with rain are more or less evenly distributed through the three months and that there is a tendency in each of the three months for the heavy rust and the medium rust years to have more rainy days than the light rust years. In two of the divisions, however, the number of days with rain in June is less in the medium rust years than in the light rust years, and less also in August in one of these divisions. It is evident, therefore, that in Western Canada years with a high number of rainy days during the growing season tend to be associated with years of medium or heavy stem-rust infection.

TABLE 12.—MEAN NUMBER OF DAYS WITH 0.01 OR MORE INCHES OF RAIN IN MANITOBA, SASKATCHEWAN, AND ALBERTA, BY METEOROLOGICAL DIVISIONS, FOR THE 3-MONTH PERIOD JUNE TO AUGUST, FROM 1916 TO 1938, FOR YEARS IN WHICH STEM RUST WAS LIGHT, MEDIUM, AND HEAVY IN THE DIVISIONS INDICATED

Meteorological Divisions	Light	Medium	Heavy	23-year period
	days	days	days	days
Manitoba				
Red River	22.0	24.3	26.2	23.5
Qu'Appelle and Assiniboine Rivers	24.7	25.0	29.0	25.7
Saskatchewan				
Qu'Appelle River	22.8	23.2	26.6	23.6
Saskatchewan Forks	25.7	30.0	—	27.1
South Saskatchewan River	20.4	26.0	—	20.9
North Saskatchewan River	24.3	24.7	—	24.4
Alberta				
Bow River	21.0	30.5	—	21.9
Red Deer River	28.3	32.0	—	29.0
North Saskatchewan River	27.9	28.5	—	28.0

The association, however, seems not to be a close one. For example, in the Red River division, the number of days with rain was below normal in 2 heavy rust years (1916 and 1923) and in 2 medium rust years (1919 and 1930), while in 4 light years (1922, 1928, 1932, and 1934) the number was above normal. In the other Manitoba divisions (Qu'Appelle and Assiniboine Rivers), 4 medium rust years had less than the normal number of days with rain and 5 light rust years had more than the normal number. In the other division, the number of light rust years with an above-average number of days with rain increased progressively westward, the Red Deer River and the Bow River divisions having each 11 years with more than the average number of rainy days. What significance a higher-than-normal frequency of days with rain during the growing season may have

on stem-rust development, would appear to depend on circumstances. It is probable that the timeliness of rain in relation to the occurrence of spore showers would be of more significance than the actual number of rainy days in a season. There is, of course, as a matter of chance, a greater probability of timeliness of rain when the days of rain are above average than when they are below average. The timeliness of rains with respect to the occurrence of spore showers will be considered further in connection with the discussion on the interrelation of factors influencing the development and spread of stem rust.

TABLE 13.—MEAN NUMBER OF DAYS WITH 0.01 OR MORE INCHES OF RAIN IN MANITOBA, SASKATCHEWAN, AND ALBERTA, BY METEOROLOGICAL DIVISIONS, FOR THE MONTHS OF JUNE, JULY, AND AUGUST, FROM 1916 TO 1938, FOR YEARS IN WHICH STEM RUST WAS LIGHT, MEDIUM, AND HEAVY IN THE DIVISIONS INDICATED

Meteorological Division	June			July			August		
	Light	Medium	Heavy	Light	Medium	Heavy	Light	Medium	Heavy
	days	days	days	days	days	days	days	days	days
Manitoba									
Red River	8.2	9.5	8.8	7.1	7.5	9.4	6.7	7.3	8.0
Qu'Appelle and Assiniboine Rivers	9.1	9.8	10.2	7.9	7.6	10.4	7.7	9.1	8.4
Saskatchewan									
Qu'Appelle River	8.7	9.7	10.2	6.9	7.2	9.2	7.2	6.2	7.2
Saskatchewan Forks	9.4	10.8	—	7.8	10.6	—	7.8	8.5	—
South Saskatchewan River	8.4	10.0	—	6.4	9.0	—	5.6	7.0	—
North Saskatchewan River	9.6	7.5	—	7.6	10.0	—	7.3	7.2	—
Alberta									
Bow River	8.2	12.0	—	6.1	10.5	—	6.6	8.0	—
Red Deer River	10.3	10.0	—	8.7	12.0	—	9.3	10.0	—
North Saskatchewan River	9.6	8.5	—	9.5	10.5	—	8.7	9.5	—

Occurrence of Mist and Fog

Wherever mist or fog is of frequent occurrence in grain-growing areas, both are undoubtedly important factors in promoting stem-rust infection. Klebahn (111) emphasizes the rôle played by fog, and Freeman and Johnson (67) assert that misty weather is particularly favourable for infection. Misty or foggy weather, although it would promote infection, would not, however, provide suitable conditions for the development of the organism within the plant tissues, as such weather is usually cool and dull, whereas warmth and sunshine, as mentioned elsewhere in this paper, are needed by the fungus to stimulate growth and spore production. If inoculum is present, a day or two of misty or foggy weather followed by bright warm days would favour stem-rust development.

Mists and fogs rarely occur in Western Canada during the growing seasons. For the years under review, records of the occurrence of mist seem to be entirely wanting, and to a large extent the same may be said of fog in all but a few districts where the local topography favours its

formation. From 1916 to 1923, fog was of more frequent occurrence at Minnedosa, Manitoba, than at any other point in the grain-growing area, but the average number of days on which it occurred from June 15 to July 30 was 4 for the light and the medium rust years and 3 for the heavy rust years During these 13 years, fog is rarely recorded at any other station in the cultivated area of Manitoba. For example, at Winnipeg, it was reported only on July 10, 1916, and on July 6 and 16, 1917. At a few stations in Saskatchewan, such as Battleford, Swift Current and Qu'Appelle, the average occurrence is 1 or less than 1 each year. After 1928, the dates on which fog occurred are not given in the meteorological reports, so that the dates of its occurrence in June and July are not known; but at Minnedosa it was not reported during these two months in any year more than 3 times and the average occurrence for the ten years is 1 per year. The highest average for any of the Saskatchewan stations is slightly less than that for Minnedosa. It would appear, therefore, that in Western Canada fog is a factor of little consequence in the promotion of stem-rust epidemics, although if viable inoculum is present where and when it occurs, it undoubtedly presents favourable conditions for infection.

Relative Humidity of the Air

Owing to the dependence of stem rust on the presence of moisture to facilitate the germination of spores and the infection of plants, it might be regarded as a logical deduction that seasons of high atmospheric relative humidity would be associated with seasons of severe outbreaks of the disease. In this connection, it would be well to distinguish between moisture present in the air as rain, mist, or fog, and moisture present as water vapour. The relative humidity of the air at any given time represents the capacity of the air to hold water in the form of vapour, and is expressed as a percentage of this capacity. It varies from day to day, and even from hour to hour, depending on the amount of water vapour present and the air temperature. If the actual amount of water vapour present in the air remains unchanged, the relative humidity falls as the temperature rises, and rises as the temperature falls. A greater or less amount of water vapour is always present in the air and it is the source of all precipitated moisture. If fog or mist is present or rain is falling, the relative humidity is high, the air being at or nearly 100% saturation. When the relative humidity and the temperature are both high, the weather is sultry and feels oppressive.

In the different studies that have been made on the relation of weather conditions to the development of stem rust, only a few give consideration to the relative humidity of the air, a fact which may mean that the relative humidity of the air—as distinct from the occurrence of precipitated moisture—during the development period of the disease, is of comparatively minor importance. Freeman and Johnson (67) show, in a comparison of the relative humidity in the Mississippi Valley during the month containing the critical period for stem rust in the several States of that area, that the relative humidity in 1903 was about normal, in 1904 about 1.6% above normal, and in 1905 approximately 6.0% above normal. Stem rust was extremely severe in 1904, but although very prevalent in 1905 was considerably less destructive than in 1904. In 1903 it was of moderate

intensity. If the intensity of infection bore a direct relationship to the height of the relative humidity, infection should have been least in 1903, which it was, and greater in 1905 than in 1904, which it was not. According to Gassner (71), the prevalence of stem rust in Uruguay is not associated with high relative humidity, as the humidity is highest in winter when the rust is least evident or absent. He points out, however, that in summer, owing to the lower temperatures at night, the relative humidity in the early morning reaches or almost reaches the saturation point every day, thus favouring spore germination and infection. Lambert (113) is inclined to the belief that the high relative humidity of the morning air in the Red River Valley in Minnesota is correlated with the occurrence of dew, a factor which he regards of much importance in the promotion of stem-rust attacks. Tiemann (218) states that in the vicinity of Breslau, Germany, in 1932, wheat became heavily rusted in July, and that for this month the relative humidity averaged 88%, an excess over that of the two previous years of 10 to 12%. Zekl (238) claims that epidemics of stem rust occur in seasons of low precipitation and high atmospheric humidity.

To ascertain if high relative humidity during the growing season is characteristic of heavy rust years in Western Canada, an examination has been made of data for several stations in this area for the 23-year period under review. Table 14 presents the general means of the average daily relative humidity for June, July, and August at Winnipeg and Minnedosa in Manitoba, at Qu'Appelle, Saskatoon, and Swift Current in Saskatchewan, and at Medicine Hat and Edmonton in Alberta, for light, medium, and heavy rust years.

TABLE 14.—MEAN RELATIVE HUMIDITY FOR THE MONTHS OF JUNE, JULY, AND AUGUST, FROM 1916 TO 1938, AT THE SEVEN STATIONS INDICATED, FOR YEARS IN WHICH STEM RUST WAS LIGHT, MEDIUM, AND HEAVY IN THE METEOROLOGICAL DIVISIONS REPRESENTED BY THE STATIONS

Station	June			July			August		
	Light	Medium	Heavy	Light	Medium	Heavy	Light	Medium	Heavy
Winnipeg	67.3	70.6	65.2	69.9	70.6	68.8	71.3	73.0	67.0
Minnedosa	73.2	76.6	74.4	72.0	76.0	79.0	76.0	77.3	77.2
Qu'Appelle	69.0	68.8	69.6	69.2	67.0	75.0	69.9	66.6	73.0
Saskatoon	62.7	64.8	—	60.7	66.4	—	64.7	69.1	—
Swift Current	62.7	71.5	—	60.4	66.0	—	61.3	66.0	—
Medicine Hat	61.6	66.5	—	56.8	63.0	—	59.7	64.0	—
Edmonton	62.4	65.0	—	66.3	70.0	—	68.7	71.0	—

The data show that the relative humidity is slightly higher at Winnipeg, but slightly lower at Minnedosa and Qu'Appelle for each of the three months in the light rust years than in the heavy rust years. At all of the stations, except Qu'Appelle, the medium rust years have a higher average relative humidity in these months than have the light rust years. On the other hand, the relative humidity is higher, except in two or three instances, in each month at Winnipeg, Minnedosa, and Qu'Appelle in the light rust years than at the other stations in the medium rust years. There seems, however, to be a slight tendency in Western Canada for seasons in which

stem-rust infection was light to have a somewhat lower average relative humidity than seasons in which infection was more pronounced. The tendency seems more evident in the more westerly parts of this area. As the differences between the average percentages of relative humidity in the light rust class of years and those in the other two classes are small in most instances, it is doubtful if the differences have had any appreciable effect on the amount of stem rust that developed. It will be seen later that the average temperatures for the respective months varied but slightly from the normal in any of the three classes of years. Perhaps, therefore, at those stations, or rather in the divisions represented by them, where there was an appreciable increase in the relative humidity during seasons of medium or severe rust infection, dews might have been slightly more frequent, or at least more copious, than normal, and, therefore, conditions for infection more favourable. The data for Winnipeg, however, show that epidemics may develop in the Red River division in seasons when the average relative humidity is slightly below that for non-epidemic seasons. The average relative humidity in the light rust years at this station is, however, somewhat higher each month than in the same years at the four most westerly stations, but it is not probable that at these stations the relative humidity of the air has been a limiting factor in stem-rust development.

Frequency of Dew

The frequent occurrence of copious dews at night during the summer months is very widely regarded as providing favourable conditions for spore germination and plant infection. For these processes, dew is obviously a better medium than rain, for dew collects gradually, wetting the plant surface uniformly, and is less likely than rain to wash off spores from the plants. Eriksson and Henning (59) and Sorauer (188) refer to a few early reports in which the occurrence of abundant dew is said to have promoted heavy rust infection, and they mention many instances in which hot sunny days followed by cool nights during summer are said to have provided conditions favourable to rust. The latter weather conditions should probably be interpreted to mean that during such periods the deposition of dew at night was abundant, although undoubtedly the warm day temperatures also had a favouring effect. Bolley (23), Klebahn (111), Freeman and Johnson (67), Roussakov (170) and some others (9, 24, 42, 71, 106, 118, 218) have emphasized the importance of heavy dews in promoting rust infection. Lambert (113) states that in some years heavy stem rust developed in parts of the Red River Valley during periods when rain was entirely absent, and he suggests that this was made possible by abundant dew formation during such periods.

Although no official records are available relative to the frequency or abundance of dew formation in Western Canada, it is a well known fact that in this region, owing to the rapid radiation that occurs at night, dews are both frequent and abundant during the summer months. To gain some idea of the approximate number of nights on which dew forms in early summer, a computation was made involving the daily temperature and relative humidity at 7.00 p.m. and the minimum temperature at night, at Winnipeg, for each day of the last two weeks of June and the first week

of July over a period of twelve consecutive years. By reference to Table 42 of the Smithsonian Meteorological Tables (Revised Addition, Washington, 1896), it was determined from these data for each day whether or not the relative humidity at 7.00 p.m. and the fall in temperature after 7.00 p.m. were sufficiently great to reduce the water-holding capacity of the air to the dew point. The relative humidity data apply to the air at a point 4 feet above ground level. As the data are only indicative, and, as their presentation would be cumbersome, they are omitted here, although those for three or four years are included subsequently in Table 26. It was found that the temperature-humidity relation was such as to indicate that, at 4 feet above ground, the air reached the dew points on from 65 to 70% of the nights during those three weeks.

On some of the nights for which dew formation is indicated, the wind velocity was too great to permit the deposition of dew, but how frequently this happened is not known, as the wind often abates considerably after sunset, and hence its velocity at 7.00 p.m. is not a very accurate index of its velocity between midnight and early morning. The number of nights, however, on which wind prevented the formation of dew in the period discussed was probably comparatively small in any particular year. On the other hand, the humidity of air within the standing crops during periods of dry weather is probably appreciably higher than that of the surrounding air, as there is considerable loss of moisture from the soil as well as from the plants themselves, and as the air amongst the plants is less subject than the air outside to disturbance by wind. Roussakov (171) found that during night in dry summers in the south-eastern Russian steppes the relative humidity in the midst of crops at a point about 4 inches above ground level is from 15 to 50% higher than that outside them at a level approximately 4 feet above ground; although, during daytime and in wet seasons, the data did not warrant the drawing of conclusions. In dry weather, the air about the upper half of the plants would probably, therefore, have a higher humidity than that outside them, and as it is from these parts that radiation is most pronounced, dew was probably present on them on some nights in which dew formation was not indicated by the humidity and temperature data.

At any rate, the deposition of dew on the plants at night is of very frequent occurrence during the summer in Western Canada. If the crops are thick and rank, as they usually are in bad rust years, dew droplets frequently persist on the more sheltered parts of the plants throughout the morning until well on toward noon. There can be little doubt that stem-rust infection in Western Canada is very definitely facilitated by the occurrence of frequent dews.

Relation of Temperature to Stem-Rust Development

The cardinal temperatures for development of the uredial, or summer, stage of stem rust have been determined under controlled conditions. Johnson (103) found that, for urediospore germination, the minimum and maximum temperatures were near 35° and 88° F., respectively, and the optimum range between 53° and 63° F. His results are in general agreement with those of Mehta (130), Stock (214), and Wilhelm (236), although these investigators, and others (36, 137, 237) found the upper limit of the

optimum range to be slightly higher, about 68° F. Sibilia (184) states that exposure of urediospores to a temperature of from 95° to 99° F. completely inhibited germination. Hwang (97) found, however, that urediospores of Race 36 of stem rust could withstand very well a temperature of 111° F. for 48 hours, but that, at 122° F., they lost vitality rapidly and all were dead within 60 hours. At 140° F., more than one-half of the spores lost their vitality in 4 hours, and none were viable after 15 hours.

For infection and the subsequent development of the organism within the host, the optimum temperature is somewhat higher than for spore germination. Stakman and Levine (208) found the best rust development between 66.5° and 70° F., while Peltier (151) found it to be somewhat higher, between 68° and 77° F., and Gassner and Straib (76), slightly lower, between 62.6° and 68° F. Mattras (124) found the optimum range to be wider, between 64.4° and 77° F., and this range corresponds closely with that at which Johnson and Newton (104) obtained best development. Vigorous stem-rust development may, therefore, be expected to take place at temperatures between 65° and 75° F.

Temperatures above or below the optimum tend to retard stem-rust development. Lauritzen (115) obtained slight infection at 45.5° F. but none at 42° F. (one experiment only). Peltier (151) states that development was practically suspended when the temperature fell to 50° F. or rose to 86° F. He observed no development at 41° F. after a period of 9 weeks. Mehta (130), however, records limited spore formation at 40° F. after 3 weeks; but, after the same lapse of time, Gassner and Straib (76) observed no evidence of development at temperatures between 46.4° and 57.2° F. They found the stem-rust fungus to be relatively resistant to the protracted action of high temperatures (86° to 95° F.), a finding supported by Johnson and Newton (104), who obtained rust development on wheat and oats at temperatures between 95° and 99° F. At these temperatures, however, development was noticeably less vigorous than at somewhat lower temperatures. Stakman and Levine (208) observed a retardation in the incubation period of 1 day for every rise in temperature of 10 degrees above 70° F. and of 1 day for every fall of 5 degrees below 66.5° F. A somewhat more pronounced retardation in rate of growth was found by Melander (137) in Race 35, which, at 68° F., produced spores normally within 10 or 11 days, but, at 50° F., within 18 days.

Although stem-rust development may become largely suspended at extreme temperatures, say, at a low of 40° F. and a high of 100° F., the organism in the host plant is not killed by these temperatures, and can resume development when temperatures become less extreme. Indeed the organism can survive much lower temperatures and considerably higher ones. Melander (137) found that the mycelium of wheat stem rust was capable of growth after storage for 80 days at temperatures just at and above the freezing point. As a matter of fact, he showed that, at this temperature, urediospore production was quite possible, although some races were better able than others to develop under such conditions. From his results, he concludes that the organism in the host tissue can withstand as low a temperature as the host plant can endure, thus confirming the earlier findings of Stakman and Levine (208). Apparently, too, the organism can survive about as high a temperature as can be tolerated by

the host. In one experiment, Stakman and Levine (208) subjected newly infected plants during the incubation period to a maximum daily temperature of 103.5° F. and a minimum daily mean of 71.1° F. and obtained a moderate degree of infection. Johnson and Newton (104) record that, in 1936, between June 27 and July 15, the temperature in the greenhouse rose as high as 116° F., the mean daily maximum being 99.6° F. and the mean daily minimum 66.8° F. Infection developed in wheat seedlings inoculated on June 27, and, although in some races of the rust, the infection types were abnormal, other races (e.g., Race 48), seemed uninfluenced by such temperatures. At a uniform temperature of 95° to 99° F., moderately good development occurred in some races but not in others. Both host and organism showed evidence of decreasing vigour at these temperatures. Cassell (36) showed that Race 15 could survive an average temperature of 105° F., with a maximum of 131° F., for 14 days.

A comparison of the optimum temperatures for the growth of the cereal host with the optimum for stem-rust development brings out an interesting relationship. It has just been seen that the optimum temperature for spore germination lies approximately between 55° and 65° F., and for stem-rust development, between 65° and 75° F. A temperature between 60° and 70° F. may, therefore, be regarded as well suited to stem rust. It was found by Peltier (151) that for eight different varieties of wheat, the best growth occurred between 59° and 68° F., and by Hutcheson and Quantz (96), that, for one variety each of wheat, oats, barley, and rye the best development occurred at 62°, 65° to 75°, 58° to 62°, and 62° F., respectively. Although the optimum temperature for cereals may vary somewhat with the species or with the variety, it may be said, in general, that the range of temperature that permits good development of the parasite also permits good growth of the hosts. Temperatures below or above the optima tend to retard, and, if the departure is sufficiently great, even inhibit growth both of the organism and of the hosts.

It would appear from the observations and studies of many different investigators that hot weather is generally associated with severe outbreaks of stem rust in the Mississippi Valley. Walster (227), in a comparison of five epidemic and five non-epidemic years, showed that during the growing season maximum temperatures rose more rapidly and reached their highest point sooner in epidemic years than in non-epidemic years. Tehon and Young (215) considered that in Illinois a mean temperature of 71.5° F. (accompanied by high humidity) was optimum for field infection. For the period 1919 to 1923, Levine (118) found a definite correlation between the mean temperature of the last two months of the growing season (July and August in Western Canada) and the severity of stem rust. The correlation coefficient, however, was rather low ($+ 0.283 \pm 0.038$). No infection developed at stations where the mean temperature was below 60° F., but heavy infection developed at stations where the mean temperature was comparatively high (ranging from 66° to 72° F.). Waldron (224, 225) points out that in North Dakota the mean temperature for July, 1916, was the hottest on record, being 4.7° F. above normal, and that for July, 1935, the next hottest. Extremely severe stem-rust epidemics occurred in both these years.

Stakman and Lambert (207), in a study of the effect of temperature on stem-rust development in the Upper Mississippi Valley (Minnesota, South Dakota, and North Dakota), found that for the period studied (1904-1925, inclusive) there was "a tendency for destructive epidemics to develop in warm growing seasons and for cool seasons to be comparatively free from rust." There were no destructive epidemics in seasons with an average temperature below 61° F., and no season with an average temperature above 64° F. escaped having one, although in seasons with intermediate temperature (61°-64° F.), stem rust was epidemic in some and not in others. Later, Lambert (113) showed that the odds were 6 to 1 that the occurrence of stem-rust epidemics in hot growing seasons was not due to chance. He pointed out, however, that in the period studied there occurred three noteworthy exceptions, namely, the years 1904, 1910, and 1916 The growing season (May, June, and July) in 1904 was moderately cool but stem rust was severe; in 1910, June and July were hot but stem rust was light; and in 1916, May and June were cool but stem rust was exceedingly destructive. In the latter year, however, the month of July was very hot.

These findings are in general agreement with those of several other investigators elsewhere. In Uruguay, Gassner (71, 72, 73) observed that stem rust flourished in the hot summer months but decreased in prevalence with the approach of autumn. Cotton (43) reports that stem rust was heavier in England in 1919 than in 1920, a condition which he attributes in part to the warmer weather of the former year. Chabrolin (37) claims that, in Tunis, a wet March followed by a dry, hot April is conducive to a heavy stem-rust attack. This observation, he states, was made much earlier by Boeuf. Zekl (238) asserts that seasons of heavy rust infections are usually characterized by great heat. Vasey, Balwin, and Doery (222) state that, in Victoria, Australia, stem rust did serious damage in 1916 and 1934. The main attack developed in the first week of November, a period of high temperatures combined with high humidity.

Cool growing seasons have usually, although not always, been regarded as unfavourable to stem-rust development. Bailey (10) suggests that the failure of stem rust to reach epidemic proportions in Manitoba in 1924 was due to the cool weather that prevailed during the latter part of the growing season. Peltier (157) states that, in Nebraska, low temperatures are apparently the major limiting factor in the development of primary infection and in the subsequent development of uredia. Johnston, Melchers, and Millar (107) are of the opinion that minimum temperatures are more important in relation to infection than are maximum or mean temperatures, as it is not until minimum temperatures become high enough to favour abundant infection that stem rust becomes severe in the State of Kansas. Melchers and Johnson (140) believe that frequent night temperatures of below 60° F. from May 15 to June 24 in 1938 were largely responsible for holding stem rust in check in Kansas in that year. On the other hand, Bolley (23) and Freeman and Johnson (67) suggest that the low temperature which prevailed during the growing season of 1904 was partly responsible for the severity of the attack which developed in the Upper Mississippi Valley in that year. Similarly, Zimmermann and Schneider (240) believe that the abnormal weather in Mecklenburg during July, 1909, when the temperature fell as low as 42° or 43° F., contributed to the development of

the severe outbreak that occurred in that year. Lambert (113) points out that stem rust may become epidemic in a cool season if other conditions favouring its development are present, as happened in 1904 in the Mississippi Valley.

Temperature in Relation to Outbreaks of Stem Rust in Western Canada

From the foregoing discussion, it is evident that temperature may profoundly influence stem-rust development. As in Western Canada stem rust is much more severe in some years than in others and in some areas than in others, temperature data have been studied to ascertain to what extent this variability in the amount of infection may be attributable to temperature conditions in the different years and areas.

Seasonal Temperatures. Temperature data for the months of May, June, July, and August are presented in Tables 15 and 16. During the month of May, temperature can have no direct influence on stem rust in Western Canada, as the disease is never present during that month. To a large extent, the same is true for the first half of June, as the disease is not usually visible in the field until towards the end of June, and in some years not until after the beginning of July. The temperature data for May and the first half of June are given consideration largely because of the influence that spring and early summer temperatures may have on crop development.

TABLE 15.—MEAN TEMPERATURE IN MANITOBA, SASKATCHEWAN, AND ALBERTA, BY METEOROLOGICAL DIVISIONS, FOR THE 4-MONTH PERIOD MAY TO AUGUST, AND FOR THE 3-MONTH PERIOD JUNE TO AUGUST, FROM 1916 TO 1938, FOR YEARS IN WHICH STEM RUST WAS LIGHT, MEDIUM, AND HEAVY IN THE DIVISIONS INDICATED

Meteorological Division	Months	Light	Medium	Heavy	23-year period
		° F.	° F.	° F.	° F.
Manitoba					
Red River	May – August	62.5	62 1	61 4	62 2
	June – August	65.3	65.4	64.8	65.2
Qu'Appelle and Assiniboine Rivers	May – August	61.3	61.1	59.7	60.9
	June – August	64.1	64.4	63.3	64.0
Saskatchewan					
Qu'Appelle River	May – August	60.1	60.7	58.6	59.9
	June – August	62.7	63.7	61.8	62.7
Saskatchewan Forks	May – August	59.7	59.5	—	59.7
	June – August	62.6	62.2	—	62.2
South Saskatchewan River	May – August	60.3	60.0	—	60.3
	June – August	63.2	63.0	—	63.0
North Saskatchewan River	May – August	58.8	59.2	—	58.5
	June – August	60.5	61.7	—	60.7
Alberta					
Bow River	May – August	58.5	58.2	—	58.5
	June – August	61.4	60.9	—	61.3
Red Deer River	May – August	57.0	56.9	—	56.9
	June – August	59.4	59.9	—	59.5
North Saskatchewan River	May – August	56.4	56.3	—	56.4
	June – August	58.6	59.3	—	58.7

TABLE 16.—MEAN TEMPERATURE IN MANITOBA, SASKATCHEWAN, AND ALBERTA, BY METEOROLOGICAL DIVISIONS, FOR THE MONTHS OF MAY, JUNE, JULY, AND AUGUST FROM 1916 TO 1938, FOR YEARS IN WHICH STEM RUST WAS LIGHT, MEDIUM, AND HEAVY IN THE DIVISIONS INDICATED

Meteorological Divisions	May			June			July			August		
	Light	Medium	Heavy	Light	Medium	Heavy	Light	Medium	Heavy	Light	Medium	Heavy
	° F.	° F.	° F.	° F.	° F.	° F.	° F.	° F.	° F.	° F.	° F.	° F.
Manitoba												
Red River	54.0	52.6	50.8	62.5	63.0	61.2	67.8	67.9	69.4	65.3	65.6	64.2
Qu'Appelle and Assiniboine Rivers	52.9	51.3	49.2	60.9	61.6	60.0	66.7	66.8	68.4	64.3	64.8	61.4
Saskatchewan												
Qu'Appelle River	51.8	51.5	48.2	59.7	61.7	58.8	65.7	65.7	66.8	62.7	64.0	60.4
Saskatchewan Forks	51.8	50.9	—	59.3	60.7	—	65.6	65.1	—	62.2	61.5	—
South Saskatchewan River	51.5	50.5	—	59.9	61.5	—	66.6	66.5	—	63.2	61.5	—
North Saskatchewan River	50.7	50.0	—	57.6	60.7	—	63.6	64.5	—	60.3	60.5	—
Alberta												
Bow River	50.6	50.0	—	58.1	58.5	—	64.4	64.5	—	61.6	60.0	—
Red Deer River	49.7	47.6	—	56.8	58.0	—	62.3	63.0	—	59.2	59.0	—
North Saskatchewan River	49.7	47.5	—	56.5	58.0	—	61.4	62.0	—	58.3	58.0	—

Table 15 contains for each meteorological division and for each class of years the general means of the average daily temperature for the 4-month period May to August and for the 3-month period June to August. From this table, it is evident that, in Western Canada, temperatures during the 3-month period, or even the 4-month period, are very satisfactory for urediospore germination, being in fact within the optimum range of temperature for this process. As pointed out earlier, this range is somewhat lower than the optimum range for the development of the organism within the host tissue. The mean temperatures for the 3-month period in the first five of the divisions lie within the latter range or near its lower limit, but in the other four divisions somewhat below that limit, although within the range at which stem rust will develop. Temperatures are usually lower in June than in July and August, and, as there is usually little stem rust present in June, the mean temperatures for the period in which stem rust is generally present (July and August) are somewhat higher in all divisions than those indicated for the three months.

A comparison of the mean temperatures for the different classes of years, shows that in the first three meteorological divisions, that is to say in the bad rust area, the general mean for the 4-month period is slightly lower in the heavy rust years than in the light rust years. The same is true of the 3-month period in these divisions. In seven of the nine divisions, the means for the 4-month period are slightly lower in the medium rust years than in the light rust years, although, in six divisions, the means for the 3-month period (June to August) are higher in the medium than in the light rust years. This fact would indicate that temperatures in May of the medium rust years were somewhat lower than those of the light rust years. Evidently then, in the bad rust area of Western Canada, there has been a tendency for the temperature to be slightly lower in heavy rust years than in light rust years On the other hand, there has been a tendency in the medium rust years for the growing season (June to August) to be slightly warmer than in the light rust years. The differences in temperatures are so small that they probably have no significance. It will be observed, however, that the mean temperature for the growing season in the heavy rust years was above the minimum temperature limit (61° F.) given by Stakman and Lambert (207) for the development of epidemics in the Upper Mississippi Valley. Medium infection, however, developed in Northern Alberta in years 1927 and 1938 when the mean temperature for the growing season was slightly below that minimum.

Monthly Temperatures. To determine what relation the average monthly temperatures of May, June, July, or August may have to the occurrence of severe outbreaks of stem rust, the temperature data for the three classes of years are summzrized by months in Table 16 for each of the meteorological divisions. In the first three divisions, the general means of of the average daily temperature for May, as well as for June and for August, is somewhat lower in the heavy rust years than in the light rust years, but for July somewhat higher. In all divisions, temperatures for the medium rust years are lower in May but higher in June than those for the light rust years, so that the average temperatures for these two months in both classes of years tend to become equalized. It appears, therefore, that cooler weather generally prevailed in the spring and early summers of

the heavy rust years than in the same months of the other two classes of years. August temperatures for the medium and for the light rust classes of years are so similar that the differences between them are probably of no significance whatever. It will be observed that medium rust development occurred in four of the divisions in years when the average temperature in August was below that usually considered satisfactory for stem-rust development.

The critical month for stem rust in Western Canada is July. Unless epidemic conditions become fairly well established in that month, damage to crops is usually of minor importance, although the year 1927 is an outstanding exception to this general rule. In Alberta, most of the development occurs in August, but as the development of stem rust in Western Saskatchewan seems to govern to a considerable extent the development in Alberta, July may be regarded as indirectly the critical month of stem-rust development in Alberta. Temperatures in July have, therefore, a direct influence on stem-rust development in the first six meteorological divisions and at least an indirect one on the other three.

In all the divisions and in all classes of years, the general temperature means for July were above 61° F. In most of the divisions, the general means for July were optimum or approximated the optimum for stem-rust development. It would seem, therefore, that in the first three divisions, which include the bad rust area, temperatures in July of the light rust years were quite suitable for stem-rust development, and were not an important deterrent in most of the other divisions. It is true that in 1916 the mean temperature for July was 60° F. in the North Saskatchewan River division of Saskatchewan, and that stem rust was comparatively light in that division, although moderately heavy in the Saskatchewan Forks division, immediately to the east of it, and severe in all of Eastern Saskatchewan. But infection was light also in the South Saskatchewan River division (south-western Saskatchewan), although the mean temperature for July of that year was 66° F. It is probable, therefore, that in the North Saskatchewan River division the failure of stem rust to reach moderate or severe proportions in 1916 was not altogether due to the comparatively low July temperature.

Whether or not in the heavy rust years the slightly higher temperature in July can be regarded as of definite significance in promoting epidemic conditions is not readily determinable. The higher temperature would tend to shorten the incubation period of each rust generation, thereby permitting more generations to be produced, but it would also tend to increase evaporation and thus remove surface moisture from the plants, thereby reducing the opportunities for infection. Furthermore, it would hasten the maturing of the crop and thus tend to offset any advantage the disease might gain from a more rapid development. The differences between the mean temperatures for July in the heavy and the light rust years are so small, being less than 2° F., that it is questionable if the differences were great enough to have any appreciable influence on the development of the disease.

Daily Minimum Temperatures. With regard to the fluctuations in daily temperatures, it may be said that summers in Western Canada are characterized by hot days and cool nights. Actually, the lowest tempera-

ture during the day usually occurs in the early morning hours, just before or after sunrise. As a general rule, day-time temperatures are sufficiently high to promote rapid stem-rust development. Any retardation of development that occurs on account of low temperatures must largely be attributed to late night and early morning temperatures. Johnston and associates (106, 107) point out that minimum temperatures have a greater influence on stem-rust development than have maximum or mean temperatures, and this view is further developed by Melchers and Johnston (140), who attribute the unusually slow establishment of stem rust in the State of Kansas in 1938 to the relatively low minimum temperatures that prevailed between May 15 and June 24, the usual period of rapid stem-rust spread in that state. These authors accept 60° F. as the minimum temperature favourable for infection and subsequent stem-rust development, and show that periods with minimum temperatures of 60° F. or above in 1938 were short and were separated by periods with unfavourable minimum temperatures, while in 1935 and 1937 periods favourable for infection were prolonged. They point out that if 55° F. were chosen as the lowest favourable temperature, the contrast between 1938 and the other two years would be still more striking. Similarly, Melchers (139) points out that in 1940 "favourable, prolonged minimum temperatures extended much further into June and July than ordinarily occurs in Kansas," and attributes to this condition the severe outbreak of stem rust in the south-central part of that state, where the wheat crop was upward of two weeks late.

The conclusion of these authors seems all the more plausible when considered in relation to the finding of Hart (81) and Hart and Forbes (82) that infection only occurs with difficulty while the stomata of the plants are closed, that is to say, from late afternoon until shortly after sunrise, and that the majority of the infections take place during the remaining morning hours, until the dew on the plants dries. As mentioned above, the minimum temperature for any given day in Western Canada is usually reached in early morning, shortly before or after sunrise. It would, therefore, appear that the inhibitory influence of a low minimum temperature would be most pronounced just about the time that the inhibition would be most effective in preventing infection, namely, when the stomata are open and dew on the plants afford moisture conditions favourable for infection. On the other hand, the ability of closed stomata to exclude germ-tubes seems to be a good deal less in some wheat varieties than in others, and in all varieties, apparently, a considerable amount of infection takes place even when the stomata are closed (82, 159). Whether or not a minimum temperature somewhat below 60° F. increases the effectiveness of closed stomata to exclude germ-tubes remains to be determined.

With a view of determining the relation of minimum temperatures to stem-rust development, a study has been made of the daily minimum temperature at four stations in Western Canada, namely, Winnipeg, Minnedosa, Qu'Appelle, and Saskatoon, from June 20 to August 4 for the three classes of years from 1916 to 1938. The four stations may be regarded as more or less representative, respectively, of the first, second, third, and fourth meteorological divisions under discussion; and the period June 20 to August 4 corresponds with the period in which stem rust first appears and becomes established in Manitoba and the eastern half of

Saskatchewan. For the sake of more exact comparison, the period June 20 to August 4 is divided into three approximately fortnightly intervals. Of the three intervals, the second and third are the most important in respect to stem-rust development. Table 17 gives the general means of the minimum temperatures for the three intervals at the four stations in the three classes of years.

There is evident in Table 17 a general tendency for minimum temperatures to be somewhat lower in the light rust years than in the other two classes of years. This tendency is, however, more evident in the first and second fortnightly intervals than in the third (July 21-August 4). In fact, at Qu'Appelle and Saskatoon, the tendency is almost reversed in the third interval, and it is in that interval that stem rust usually makes its most rapid increase in eastern Saskatchewan. This fact would seem to indicate that the lower minimum temperatures in the other two intervals and the lightness of the stem-rust attack were not very closely related in the light rust years. This view is supported by the fact that the general means for the three intervals are higher (except in one instance) at Winnipeg in the light rust years than they are for the same respective intervals at the other three stations in the medium or heavy rust years. It would be expected that if the comparatively low minimum temperatures in the light rust years were mainly responsible for holding the disease in check at Winnipeg, the still lower minimum temperatures at the other three stations in the medium and heavy rust years ought to have curtailed stem-rust development to a greater extent. Instead, however, of any marked curtailment in the amount of infection due to the lower minimum temperatures at these three stations, moderate or severe epidemic conditions developed.

TABLE 17.—GENERAL MEANS OF THE MINIMUM TEMPERATURES FOR THE PERIODS JUNE 20 TO JULY 4, JULY 5 TO JULY 20, AND JULY 21 TO AUGUST 4, FROM 1916 TO 1938 AT WINNIPEG, MINNEDOSA, QU'APPELLE, AND SASKATOON, FOR YEARS IN WHICH STEM RUST WAS LIGHT, MEDIUM, AND HEAVY IN WESTERN CANADA

Station	Period	Light	Medium	Heavy
		°F.	°F.	°F.
Winnipeg	June 20 – July 4	53.1	55.8	55.8
	July 5 – July 20	56.3	58.3	59.6
	July 21 – Aug. 4	55.9	55.5	56.4
Minnedosa	June 20 – July 4	49.5	52.5	51.6
	July 5 – July 20	52.5	54.5	56.7
	July 21 – Aug. 4	52.1	51.3	53.7
Qu'Appelle	June 30 – July 4	49.2	53.3	51.1
	July 5 – July 20	52.4	53.9	55.1
	July 21 – Aug. 4	51.6	51.0	51.5
Saskatoon	June 20 – July 4	49.7	52.4	—
	July 5 – July 20	52.9	54.3	—
	July 21 – Aug. 4	52.5	52.4	—

From the data of Table 17, it may be inferred that the percentage of days, between June 20 and August 4, with a minimum temperature of 60° F. or higher was less in the light rust than in the medium or the heavy

rust classes of years. This relationship is most pronounced at Winnipeg, less so at Minnedosa, and almost or completely disappears at Qu'Appelle and Saskatoon. The percentage of days with minimum temperatures of 60° F. or higher, for the light, medium, and heavy rust classes of years was respectively, 23, 30, and 37% at Winnipeg; 11, 15, and 20% at Minnedosa; 12, 11, and 14% at Qu'Appelle; and 11 and 11% for the first two classes at Saskatoon.

These data, however, do not take into account the distribution of such days. Melchers and Johnston (140) and Melchers (139) emphasize the particularly favourable influence on infection of the occurrence of extended periods in which the minimum temperature did not fall below 60° F., that is to say, periods of several or more consecutive days with such temperatures. By way of summarizing the data germane to this point for the 23 years under review, it may be said that for the light medium, and heavy rust classes of years, respectively, the average number of periods of 2 days or more on which the minimum temperature was 60° F. or higher per year between June 20 and August 4 was, for Winnipeg, 2.5, 3.1, and 4.4 days; for Minnedosa, 1.0, 1.1, and 2.2; for Qu'Appelle, 1.1, 0.8, and 1.6; and, for Saskatoon, 0.8 and 0.8 (light and medium rust classes). From these data, it is evident that, except at Winnipeg, there was very little difference in the average number of such periods for the light and medium classes of years. It is evident, too, that the average number of such periods per year was greater at Winnipeg in the light rust years than at Minnedosa in the heavy rust years, and still greater than Qu'Appelle.

If a period of 3 consecutive days with minimum temperatures of 60° F. or higher is considered, the average number of periods per year are reduced, being for the light, medium, and heavy rust classes of year, respectively, as follows: for Winnipeg, 1.1, 2.1, and 2.8 days; for Minnedosa, 0.6, 0.8, and 1.2 days; for Qu'Appelle, 0.5, 0.0, 0.2 days; and for Saskatoon, 0.4 and 0.2 days (light and medium rust classes).

The data just presented for Winnipeg, and to a lesser extent those for Minnedosa, seem to support the view that years with a high frequency of periods with minimum temperatures of 60° F. or above tend to be associated with years of heavy infection. And, indeed, from what is known of the relation of temperature to infection, this would be expected. On the other hand, at Qu'Appelle, and more so at Saskatoon, the data are less in agreement with this view, and, to some extent, they are contradictory to it. Only on one occasion (July 15 to 22, 1923) in the five heavy rust years was there at Qu'Appelle a period of three or more consecutive days on which the mean minimum temperature was 60° F. or higher. There was none in the medium rust years. If such periods were necessary to promote severe infection, no epidemics would be expected to have occurred in the area represented by this station. At Saskatoon, in the nine years that stem rust was of moderate intensity in that area, there was only one occasion (July 8 to 10, 1916) on which the minimum temperature was 60° F. or higher on 3 or more consecutive days; and only on seven occasions in those years had 2 consecutive days such minimum temperatures. At none of the stations, except Winnipeg (June 27 to 30) and Qu'Appelle (August 13 and 14), in 1927 was there any period of 2 or more consecutive days with minimum temperatures of 60° F. or higher between June 20 and August 30,

yet epidemic conditions were fairly well established by the middle of August in Manitoba and by the end of August in eastern Saskatchewan. The single period of 4 days (June 27 to 30) at Winnipeg had little influence on the development of stem rust, as inoculum was scarce at that time, but it is very likely that the 2-day period (August 13 and 14) at Qu'Appelle had a definite influence in promoting infection, as inoculum was then abundant. In 1938, as Figure 8 shows, only on one occasion (July 3 to 6) was the minimum temperature between June 20 and August 10 at Minnedosa 60° F. or higher for 2 or more consecutive nights, and only on two occasions at Qu'Appelle. During most of the time, minimum temperatures were considerably below 60° F. The likelihood is, however, that much infection did occur during the periods just indicated, as it is known (Table 2) that inoculum was plentiful shortly before or on those days.

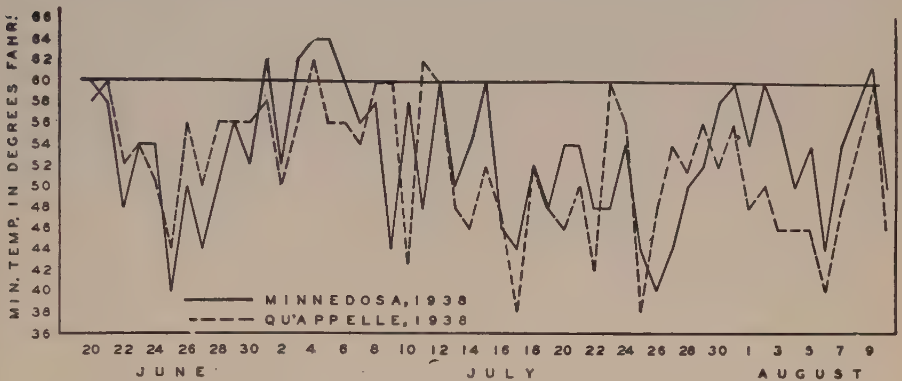

FIGURE 8. Graph showing daily minimum temperatures (in degrees Fahrenheit) from June 20 to August 9, 1938, at Minnedosa, Man., and Qu'Appelle, Sask.

There is a relationship, at least a partial one, involved in this general question of the influence of high minimum temperatures on the amount of infection, and it is, namely, that periods of high minimum temperatures sometimes, but not always, accompany periods of south wind, and periods of south wind occurring between June 20 and August 4 are not infrequently associated with spore showers of stem rust. The amount of inoculum present during some of the periods of high minimum temperatures is, therefore, likely to be greater than when the minimum temperatures are low and the wind is from some other direction. This relationship will be touched on later in connection with the interrelation of different meteorological factors on stem-rust development.

Unfortunately, there seems to be no experimental evidence to show to what extent or in what manner comparatively short daily exposures to temperatures somewhat below 60° F. interfere with stem-rust infection, or even that such exposures actually do reduce the amount of possible infection. Only occasionally in Western Canada would the temperature fall low enough in summer to interfere with urediospore germination, as the optimum for this process seems to lie between 53° and 63° F., and some germination occurs at as low a temperature as 35° F., and even just above the freezing point (137). Minimum temperatures, therefore, between 50° and 60° F. could hardly be expected to interrupt seriously the entrance of

the germ-tubes into the stomata, unless, indeed, such temperatures make the stomata more resistant to penetration of the germ-tubes. In at least some races of stem rust, infection proceeds readily below 60° F. For instance, Peltier (151) found that the lower limit for optimum infection with Race 9 on certain wheat varieties in the heading stage was 50°, and with Race 3, it was 57° F., while Melander (137) states that Race 35 of wheat stem rust, Race 2 of oat stem rust, and Race 7 of rye stem rust, respectively, readily infected seedlings of wheat, oats, and rye at the former temperature. Stakman and Levine (208) found that infection would take place at as low a temperature as the host plant could stand. It is true, of course, that growth of the organism in host tissue is appreciably slowed down at temperatures of 60° F. or less, and, at about 50° F., is generally largely suspended. This suspension of growth may possibly be mainly due to nutritional difficulties, and if so would not probably affect the germinating spore or the growth of the germ-tube on the surface of the plant. Apparently it might be easier to explain the observed retardation in the increase of stem rust by attributing it to the effect of minimum temperatures of less than 60° F. on the organism after it has penetrated through the stomata, rather than to any appreciable failure of the germ-tubes to gain entrance into the plants because of such temperatures. The effect of the higher minimum temperatures may be largely to favour the rapid establishment and promotion of the parasitic relation of host and organism.

Relation of Light to Stem-Rust Development

Light is essential for the growth of chlorophyll-bearing plants, and, as the stem-rust fungus cannot maintain itself apart from its hosts, it is evident that light is indispensible, at least in an indirect way, to the development of the disease. Furthermore, the stomata of plants open as a response to light and may thereby facilitate the entrance through them of the germ-tubes, a primary requisite of infection. Germination, of course, must first take place. Arthur (7) states that the germination of rust spores proceeds more freely at night. Bruschetti (28) claims that, in his experiments, neither light nor darkness had any influence on the germination of urediospores, while Sibilia (184) found that urediospores of stem rust, as well as of three other cereal rusts, did not germinate in the absence of light. At the time this section was being written, the author dusted freshly collected stem-rust urediospores on tap-water contained in a watch-glass, placed the watch-glass in a cabinet, inverted a small earthenware jar over the watch-glass, and shut the door of the cabinet. The spores were, therefore, in extreme darkness, but, in less than 3 hours, from 30 to 40% of the spores were showing vigorous germ-tubes with a length of two, three, and four times the diameter of the spores.

On the other hand, bright sunlight directly affects the germinability of urediospores during exposure, although the effect seems to be only temporary and not detrimental. Bolley (22) found that urediospores exposed on a watch-glass to bright sunshine in August for 21 hours fell in germination from 90 to 100% to 8 to 15%. In this instance, the injury was probably largely due to heat and rapid desiccation rather than to any direct effect of light; for later Bolley and Pritchard (24) exposed spores to sun and air during the entire month of August and found over 5% of the spores

germinable at the end of the month. Stock (214) found that urediospores of leaf rust of wheat and of rye, and of crown rust, germinated equally well under the illumination of a 500-watt lamp as in darkness, but that the germination of urediospores of stem rust was retarded under the light, and development only reached parity with that of the spores in darkness after 8 hours. Weston (234, 235) showed that urediospores of stem rust do not germinate while exposed to bright direct sunlight or to very strong diffuse sunlight. The germinability of the spores was, however, not adversely affected, for the same spores germinated afterwards when they were placed in darkness or subdued light. He states that exposure (on the surface of water) for several hours to direct sunlight when the day temperature is high may kill urediospores, but points out that the killing is due to heat, not to light. Gassner and Straib (76) found that urediospores are little affected by exposure to direct sunlight. On the other hand, Hwang (97) found a direct relation between low light intensity and retention of spore viability. At low light intensities (daily maximum 1,500 foot-candles), the germination of urediospores was reduced to about 10% after an exposure to sunlight for 270 hours, while, at moderately high light intensity (daily maximum 7,000 foot-candles), it was reduced to 10% by an exposure to sunlight for 75 hours.

To what extent the entry of the fungus into the host may be affected by light seems unclear. Gassner (71) obtained just as good infection on plants that were shaded in a room as on those exposed to light. Stakman and Piemeisel (212) state that, owing to the usually more favourable moisture conditions, best infection usually occurs at night. Lauritzen (115) found as high a number of plants infected among those incubated for 24 hours in darkness as among those incubated for the same number of hours in the greenhouse where they were exposed to the light prevailing at the time of the experiment, namely, that of cloudy winter days. His results are similar to those obtained by Stakman and Levine (208) with plants incubated in low and high light intensities. In neither case is the number of infections per plant indicated. With plants kept in incubation chambers for 48 hours in darkness, in different artificial light intensities, and in sunlight, Peltier (155) obtained as many plants infected and as much infection per plant on those plants incubated in darkness as in those incubated in sunlight or under the artificial lights. Gassner and Straib (76), on the other hand, obtained very weak infection in plants subjected to darkness for 2 days after inoculation and no infection in those subjected to 4 days of darkness after inoculation, while, in those kept under clear glass, good infection resulted. Hart (81) and Hart and Forbes (82) observed a marked reduction in the number of infections on several wheat varieties kept in darkness during the incubation period following inoculation. They attribute this result, not to any failure of the spores to germinate in darkness, but to the inability of the germ-tubes to enter the stomata, which remain closed in response to the darkness. On some varieties the inhibitory effect of darkness was more pronounced than on other varieties. Peterson (159), however, obtained satisfactory infection on certain strains of wheat under conditions of darkness. As suggested earlier, the amount of infection on certain strains of wheat under conditions of darkness may possibly vary somewhat with the host varieties used in the test, and of

course with the suitability of the moisture and temperature conditions in the incubation chambers. Further elucidation of the effect of darkness on stem-rust infection would seem necessary.

With regard to the development of the organism in the host tissue, there is general agreement that bright light induces most vigorous and rapid growth. Gassner (71) showed that strong light increased the susceptibility of the host, or, in other words, promoted vigorous rust development. Stakman and Piemeisel (212) state that a considerable amount of sunlight is necessary for best rust development, and that cloudy weather may lengthen the incubation period by a week or more. Shaded plants were invariably more weakly infected than those exposed to direct sunlight. Stakman and Levine (208) found that stem rust developed better in fairly high light intensities than in lower light intensities, and Peltier (155), that best development occurred in strong light. Gassner and Straib (76) by supplementing the low sunlight in winter by means of a 1,000-watt lamp, shortened the incubation time of the rust by from 1 to 2 days. Periods of darkness subsequent to inoculation lengthened the time of incubation. Forward (63) showed that exposure to darkness after inoculation delayed pustule formation proportionately to the length of the exposure to darkness. Melander (137) found that a reduction in light intensity retarded rust development. Levine (118) concluded from his study (which embraced stations in the Upper Mississippi Valley and Western Canada) that in the years 1919 to 1923 the normal light intensity during the growing season appeared quite sufficient for the best development of stem rust. Butler and Hayman (32) and Moreland (143) point out that in India heavy rust infection usually occurs in cloudy seasons, but from their accounts the infection seems to be influenced by the greater moisture associated with the cloudiness rather than by the decrease in bright sunshine, of which there is probably an ample amount for stem-rust development in any year. Lambert (113) states that in the Mississippi Valley stem-rust epidemics seem to occur in years that have the greatest number of clear days during the growing season, but he considers that this relationship may probably be only incidental, the more likely reasons being the higher temperature and the more abundant dews in such seasons. To insure satisfactory stem-rust development, it is now a well established practice in the more northerly latitudes to supplement the daylight of the short winter days by means of artificial illumination.

The growth response of the organism to light seems to be very closely associated with that of the host plant. As suggested by Stakman and Levine (208) and by Peltier (155), the effect on the organism is probably largely indirect. In bright light, the metabolic activity of the host plant is greater than in subdued light and as a consequence the nutritional requirements of the fungus are more adequately supplied.

The general experience that stem rust develops best in bright sunlight is not without its exception. Hart and Zaleski (83) found that under conditions of shade, plants of Hope wheat, a variety possessing a high degree of mature-plant resistance, became heavily infected with Race 21 of wheat stem rust, while similar plants of this variety exposed to normal summer sunlight were relatively free from infection. Johnson and Newton (105) showed that pronounced reduction in light intensity (60%) or in

daily hours of light during the growing period of the plants tended to lower the resistance of Hope wheat to Race 21 of stem rust, but concluded that deficiency of light decreased resistance only in conjunction with other factors that tended to induce greater succulence of the plant tissue.

Sunshine Hours in Western Canada

In the present study, consideration has been given to the total hours of sunshine for the three months June, July, and August at six stations situated within the zone severely affected by stem rust. The stations are Morden, Winnipeg, and Brandon in Manitoba, and Qu'Appelle, Indian Head, and Rosthern (40 miles north of Saskatoon) in Saskatchewan. Table 18 summarizes the data for the period from 1916 to 1938. From this table, it will be seen that the average number of hours of sunshine gives little indication as to which group of years had heavy rust attacks. For the individual months at the different stations, the respective means for June and July in the light rust years are as high as, or higher than, those in the heavy rust years, while in August the tendency is for the heavy rust years to have a somewhat higher number of hours of sunshine than the light rust years. The differences, however, appear to be too small to have any appreciable influence on the development of the disease in the crop. It seems, therefore, unlikely that in Western Canada the amount of sunshine has been more favourable to stem-rust development in one class of years than in another.

TABLE 18.—MEAN HOURS OF SUNSHINE FOR JUNE, JULY, AND AUGUST, FROM 1916 TO 1938, AT MORDEN, WINNIPEG, AND BRANDON IN MANITOBA, AND AT QU'APPELLE, INDIAN HEAD, AND ROSTHERN IN SASKATCHEWAN, FOR YEARS IN WHICH STEM RUST WAS LIGHT, MEDIUM, AND HEAVY IN MANITOBA AND EASTERN SASKATCHEWAN

Station	June			July			August		
	Light	Medium	Heavy	Light	Medium	Heavy	Light	Medium	Heavy
	hr.	hr.	hr.	hr.	hr.	hr.	hr.	hr.	hr.
Morden	254	237	255	302	295	290	271	282	291
Winnipeg	258	255	256	306	285	296	269	278	278
Brandon	239	235	215	293	283	279	268	272	267
Qu'Appelle	275	281	258	328	337	321	289	297	290
Indian Head	222	234	215	291	301	284	247	261	262
Rosthern	276	268	—	335	328	—	283	285	—

RELATION OF WIND TO STEM-RUST DEVELOPMENT

The possibility that spores of cryptogamic plants may be carried long distances by winds or air currents was suggested as early as the opening of the nineteenth century, and since that time this means of spore dispersal has become more and more recognized as the principal one by which stem rust spreads. In 1805, Banks (11) surmised that the time necessary for rust infections to produce spores(?) is short, and says "if so, how frequently in the latter end of the summer must the air be loaded as it were with this animated dust, ready, whenever a gentle breeze, accompanied with humidity, shall give the signal to intrude itself into the pores of thousands of acres of corn." Darwin (49), from reports by others, and from his own observations of dust falling on ships several hundred miles out at sea, concluded that no one need be surprised at the wide dispersion of fungus

spores by wind. More recently, the importance of wind-borne spores in connection with the spread of cereal rusts was pointed out by Bolley (22, 23), and stressed by Klebahn (110, 111), Freeman and Johnson (67), and others. Within the last two decades, evidence both circumstantial and direct has been obtained which shows that the spread of stem rust from field to field and from one area to another is almost entirely brought about by winds. Lambert (113) was the first to attempt a comprehensive study of the relation of winds to outbreaks of stem rust; but, before further consideration is given to this aspect of the study, a brief explanatory statement should be made concerning wind direction.

Wind Direction Dependent on Position of Air-Pressure Areas

Wind is the result of the unequal distribution of air pressure over the earth's surface. Meteorological Services of different countries indicate the distribution of air pressure day by day for their particular region on the daily weather maps published by such Services. These maps show, for the regions concerned, the areas having high or low air pressure on the date of issue. Areas of high and of low air pressure are indicated by successive encircling lines, called "isobars," each of which passes through points of equal air pressure (reduced to sea level) in each air-pressure area. In a high pressure area, the air pressure is highest at the centre and decreases outward; while, conversely, in a low pressure area, the air pressure is lowest at the centre and increases outward. Each successive isobar represents an equal decrease, or increase, in air pressure. There is, therefore, a decreasing air-pressure gradient from the centre of a high pressure area to the centre of a neighbouring low pressure area. The positions of high and low air-pressure areas in North America are seldom stationary, but move across the continent in a general west-to-east direction. As a rule, a high pressure area succeeds a low pressure area, and a low a high, although their relative positions may change a good deal from day to day. In a high pressure area, the direction of the wind is clockwise and more or less parallel to the isobars, but inclining slightly outward from the centre. In a low pressure area, the wind moves in the opposite direction, namely, counter-clockwise, and more or less parallel to the isobars, but inclining inward towards the centre (Figure 9). The closer the isobars are to one another, that is to say, the steeper the air-pressure gradient, the greater is the wind velocity.

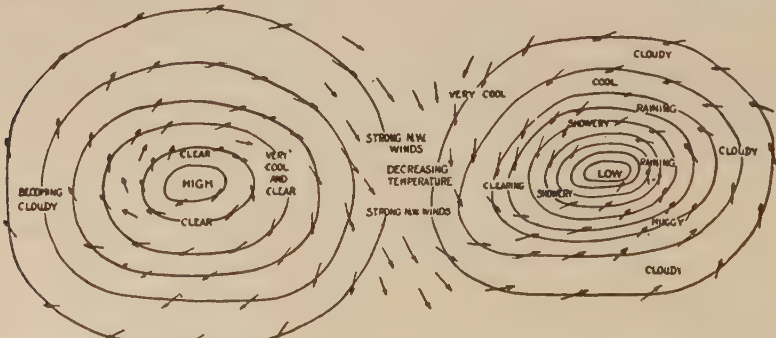

FIGURE 9. Diagrammatic representation of air-pressure distribution, showing associated wind directions and weather conditions. (After Patterson).

From what has been said, it is evident that if a low pressure area is following a high pressure area across this continent, the general direction of the wind between their centres will be from south to north. If, therefore, as they move eastward, their central portions occupy positions in the general region of the International Border, the direction of the wind, at all points in the southern part of Canada lying between the centres of the two pressure areas, will be southerly.

In the investigation already referred to, Lambert (113) studied the daily weather maps of the period May 20 to June 10, for the years 1901 to 1926, to ascertain on what days conditions were favourable to blow stem-rust spores from Texas northward to the spring-wheat area of the Upper Mississippi Valley, that is to say, on what days there was low air pressure to the west and high air pressure to the east of the Mississippi River, with more or less parallel isobars running north and south between them. He was unable to find any correlation "between the years in which conditions seemed to be the most favourable for the migration of rust from the south to the north and the years in which epidemics developed in the spring wheat area." He points out, however, that "southerly winds often sweep up the Mississippi Valley at the time the rust is most plentiful in the south, with sufficient velocity to carry spores from Texas to the spring wheat area in less than three days."

South Wind in Relation to Spore Showers

In the present study, with a view to ascertaining if any relation could be found to exist between the occurrence of south winds and the prevalence of stem-rust spores in the air over a part at least of Western Canada, an examination of the daily weather maps for the period June 12 to July 20, from 1916 to 1938, was made to determine on what dates the low pressure and the high pressure areas were so positioned as to bring a south wind to southern Manitoba. The dates are indicated in Table 19. The period June 12 to July 20 was chosen for the reason that before June 12 very few spores have been found on the slides, and after July 20 local inoculum has been usually sufficient in southern Manitoba to cause uncertainty as to whether a sudden increase in the number of spores on the slides should be attributed to wind-borne spores or to locally produced ones. Southern Manitoba was chosen because it is the area in which spores are earliest found on the slides, and in which stem rust almost invariably makes its first appearance in the field. If any association exists between winds and the prevalence of spores in the air, it should be most evident in this area, for Manitoba lies directly north of a cereal-producing region that extends from Texas northward to the Canadian border, and in that region stem rust is present in the south during early spring (April and May) and in the north during the latter part of June and throughout July (113). South winds that blow into Manitoba during June and July must pass over a rust-infected area, although in this area the severity of the infection varies greatly from year to year.

TABLE 19.—DATES ON WHICH LOW AND HIGH ATMOSPHERIC PRESSURE AREAS WERE IN SUCH A POSITION AS TO BRING A SOUTH WIND OF TWELVE HOURS OR MORE TO SOUTHERN MANITOBA BETWEEN JULY 12 AND JULY 20 OF THE YEARS 1916 TO 1938*

Date	1916	1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938
June 12	+	+	+	+	+	+	+	0	0	+	0	0	0	+	+	+	0	0	+	0	+	0	+
June 13	0	0	0	0	0	+	0	0	0	+	0	0	0	+	+	0	+	+	+	0	+	0	+
June 14	0	0	+	0	0	+	+	0	0	0	0	+	+	+	+	0	0	+	0	0	0	0	0
June 15	0	+	+	0	0	+	0	0	+	0	+	+	+	+	0	+	0	0	0	0	+	+	0
June 16	0	0	0	+	0	+	0	+	0	+	0	+	0	+	0	+	+	0	+	0	0	+	0
June 17	0	+	0	+	0	+	+	+	0	0	0	+	+	+	+	+	+	+	0	0	0	+	+
June 18	0	0	0	0	+	0	+	+	0	+	0	+	0	+	+	+	0	+	0	0	+	+	+
June 19	0	0	+	0	+	0	0	0	+	0	+	+	0	+	+	0	+	0	0	0	0	+	+
June 20	0	0	0	0	+	+	+	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	+
June 21	0	0	0	+	0	+	+	0	+	+	0	0	0	+	0	0	0	0	+	0	0	0	0
June 22	0	0	+	+	0	0	+	+	0	0	0	0	0	0	0	0	0	0	+	0	0	+	0
June 23	+	+	0	0	+	0	0	+	+	0	0	0	0	0	0	+	+	0	0	+	0	+	0
June 24	0	+	0	+	+	0	0	+	0	0	0	0	0	0	+	+	0	0	0	+	+	0	0
June 25	0	+	+	0	+	0	+	0	0	0	0	0	0	0	0	+	+	+	0	+	0	+	0
June 26	0	+	0	0	+	0	0	+	0	0	+	+	0	+	0	+	0	+	+	0	0	0	0
June 27	0	+	+	+	0	0	+	0	0	+	+	+	+	+	0	+	0	+	+	0	0	0	+
June 28	0	0	0	+	0	+	0	0	0	0	0	0	+	0	0	+	0	0	0	+	+	0	+
June 29	+	+	0	+	0	+	0	+	0	+	0	+	0	0	+	0	0	+	+	+	+	0	+
June 30	+	+	0	+	0	+	0	+	0	+	+	+	+	0	0	0	0	0	0	+	+	+	+
July 1	0	0	+	0	0	+	0	0	0	+	0	0	+	0	+	0	0	+	+	+	0	+	+
July 2	0	0	+	+	0	+	0	+	+	+	0	0	+	+	+	0	+	+	0	+	0	0	0
July 3	+	+	+	0	+	+	+	0	+	0	+	+	0	+	+	0	+	+	+	0	0	0	+
July 4	+	+	+	0	+	+	+	0	+	+	0	+	0	0	0	0	+	+	0	+	+	0	+
July 5	+	+	0	0	0	+	0	0	+	+	0	+	+	0	0	0	0	0	+	0	+	+	+
July 6	0	+	0	0	0	+	0	+	+	0	+	0	0	+	0	+	0	+	0	0	+	0	+
July 7	0	+	+	0	0	+	0	0	+	0	+	+	0	0	+	0	0	0	+	+	+	0	0
July 8	+	0	0	0	0	0	+	0	+	+	0	0	0	0	0	0	+	+	+	+	0	+	0
July 9	+	0	0	0	0	+	0	0	+	+	0	0	0	+	+	0	0	+	0	+	0	0	+
July 10	0	+	0	+	0	0	0	0	+	+	0	+	0	+	0	+	0	+	+	0	+	0	0
July 11	0	0	+	0	0	0	0	0	+	0	0	0	0	+	0	+	+	0	+	0	+	0	+
July 12	+	0	+	+	0	0	+	0	+	+	0	+	0	+	0	+	0	+	0	0	+	0	+
July 13	+	0	0	+	0	0	+	+	+	0	0	0	0	0	0	+	0	0	+	0	0	0	0
July 14	+	0	0	0	0	0	+	0	0	0	+	0	+	0	+	0	+	0	0	0	+	0	0
July 15	0	0	0	0	0	+	0	0	+	0	0	0	+	+	+	0	+	0	0	+	0	0	0
July 16	0	0	0	+	+	+	0	+	0	0	+	0	0	+	0	0	0	0	+	+	+	0	0
July 17	0	+	0	+	0	+	0	+	0	+	0	+	0	0	0	0	+	+	+	0	0	0	0
July 18	+	+	+	+	+	0	0	+	0	+	+	0	+	0	0	0	0	0	0	+	0	+	+
July 19	+	0	0	+	+	0	+	0	+	+	0	+	0	+	0	0	0	+	0	+	0	+	0
July 20	+	0	0	0	0	+	+	0	+	0	0	+	+	+	+	0	0	0	0	0	0	0	0
Total	15	18	15	18	13	23	17	15	21	19	11	19	13	22	16	16	14	19	18	16	17	14	19

* Such dates are indicated by the + sign.

It would, therefore, be expected that a sudden increase in the number of spores in the air over southern Manitoba would be associated with a period of south wind. That this is so is clearly brought out by a comparison of Tables 2 and 19. Two outstanding examples of this association may be mentioned by way of illustration, namely, June 12 to 19, 1929, and June 23 to July 2, 1935. It will be seen from Table 19 that during those periods the wind was prevailingly from the south, and, from Table 2, that pronounced increases in the number of spores are associated with these periods. The positions of the two main air-pressure systems on June 17,

1929, and on June 23, 1935, are shown respectively in Figures 10 and 11. It will be seen from these figures that the air-flow between the

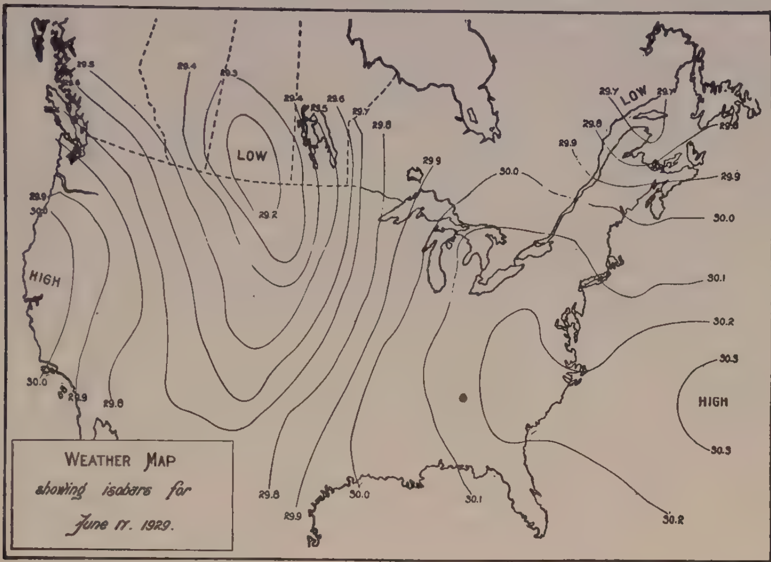

FIGURE 10. Air-pressure distribution in Canada and the United States on June 17, 1929. The closeness of the isobars east of the center of low pressure indicates a steep air-pressure gradient and strong (southerly) wind.

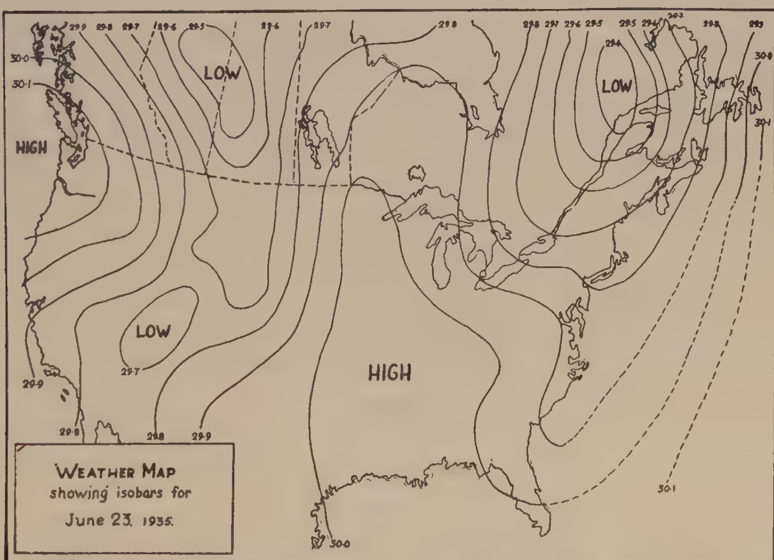

FIGURE 11. Air-pressure distribution in Canada and the United States on June 23, 1935. The wind direction is southerly in Manitoba and eastern Saskatchewan.

two air-pressure areas would cover a great part of the Mississippi Valley and, being from the south, would carry spores from there northward directly into Manitoba. Further examination of the two tables will show that, in practically every instance where there was a sudden increase in the

number of spores present on the slides, there occurred associated with this increase a period of south wind.

This association between spore showers and periods of south wind is further shown by the number of leaf-rust (*Puccinia triticina* Erikss.) spores on the slides. As each slide was examined for stem-rust spores, a record was made of the number of leaf-rust spores present. Usually leaf-rust spores appear somewhat earlier than stem-rust spores on the slides, but it is clear that there is a very close correlation between the occurrence of spore showers of leaf rust and of stem rust. Table 20 gives the number of

TABLE 20.—HOURS OF SOUTH WIND (SW., S., SE.) EACH DAY AT WINNIPEG, AND NUMBER OF UREDIOSPORES OF STEM RUST AND OF LEAF RUST INTERCEPTED DAILY BY ONE SQUARE INCH OF GLASS SLIDE EXPOSED AT WINNIPEG FROM JUNE 12 TO JULY 20, IN THE YEARS 1927, 1929, 1932, 1935, AND 1938

Date	1927			1929			1932			1935			1938*		
	South Wind	Stem Rust	Leaf Rust	South Wind	Stem Rust	Leaf Rust	South Wind	Stem Rust	Leaf Rust	South Wind	Stem Rust	Leaf Rust	South Wind	Stem Rust	Leaf Rust
	hr.	no.	no.	hr.	no.	no.	hr.	no.	no.	hr.	no.	no.	hr.	no.	no.
June 12	0	0	0	19	0	8	9	0	0	0	0	0	17	0	0
June 13	0	1	0	14	0	1	13	2	1	5	0	0	24	—	—
June 14	22	2	1	13	0	2	1	2	0	0	0	0	6	5	42
June 15	24	0	26	13	24	118	6	1	0	5	0	0	0	—	—
June 16	24	1	16	15	109	240	22	2	14	0	0	0	5	0	0
June 17	24	0	20	24	193	736	20	0	1	3	0	0	23	—	—
June 18	15	0	0	23	0	5	3	0	0	8	0	0	24	0	14
June 19	16	0	0	15	0	0	17	0	6	2	0	1	24	—	—
June 20	5	0	0	4	0	2	6	0	5	2	0	0	24	18	430
June 21	0	0	19	12	0	0	6	0	0	0	0	0	8	—	—
June 22	0	2	0	0	0	0	0	1	1	1	—	—	0	10	11
June 23	11	0	16	2	0	0	18	0	1	24	9	8	0	—	—
June 24	7	3	17	0	0	0	11	1	4	24	240	126	0	0	0
June 25	8	7	63	0	0	2	12	0	7	20	52	64	0	—	—
June 26	24	24	193	18	0	0	6	0	3	5	0	0	3	1	4
June 27	18	20	1150	12	0	0	5	0	0	0	0	6	15	—	—
June 28	11	0	2	9	1	2	2	—	—	23	10	9	24	86	110
June 29	23	4	10	11	0	1	0	—	—	24	16	41	24	—	—
June 30	12	0	8	10	0	0	9	1	2	23	38	79	14	328	451
July 1	0	0	3	1	0	0	0	1	1	24	8	10	22	—	—
July 2	9	0	1	17	0	0	17	0	0	17	21	32	0	2	43
July 3	23	0	5	16	2	8	12	0	0	5	7	3	18	—	—
July 4	19	38	23	3	0	2	20	0	0	18	12	5	17	0	21
July 5	21	22	37	0	0	0	3	0	1	0	5	4	20	—	—
July 6	1	0	0	21	4	10	0	0	0	2	0	2	15	4	116
July 7	21	11	15	7	—	—	6	0	0	19	1	3	2	—	—
July 8	5	7	0	3	3	12	14	8	24	17	0	0	0	3	180
July 9	0	0	0	13	2	8	1	1	1	15	3	0	17	—	—
July 10	20	0	11	23	481	1438	0	0	0	10	0	0	5	140	810
July 11	10	3	13	24	283	1029	13	10	18	3	3	2	23	—	—
July 12	13	1	2	22	0	0	1	0	2	0	12	2	16	247	1430
July 13	3	0	8	9	31	112	8	1	9	1	7	4	0	—	—
July 14	11	3	0	3	—		23	2	0	9	6	5	7	113	920
July 15	0	0	7	18	113		14	0	3	14	51	10	3	—	—
July 16	0	1	13	23	4		0	4	8	22	1124	146	2	390	1840
July 17	12	4	30	0	3	Numerous	15	7	17	1	5	3	2	—	—
July 18	1	6	8	0	34		9	15	25	13	380	66	16	880	4360
July 19	23	193	702	24	845		6	13	7	14	147	22	0	—	—
July 20	24	61	79	24	2138		0	80	80	3	357	182	0	200	82

* In 1938, the exposures were of 48 hours duration instead of 24 hours.

hours of south wind (S.E., S., S.W.) each day at Winnipeg, together with the number of leaf-rust and stem-rust urediospores on the slides exposed at Winnipeg from June 12 to July 20 for two light and three heavy rust years. The two periods just mentioned above are striking examples of this correlation.

As mentioned before, spores in the air are present earlier and are more numerous in June and July in southern Manitoba, especially in the Red River Valley, than elsewhere in Western Canada because this area lies directly in the path of south winds which sweep over that vast grain-growing area west of the Mississippi River. In Saskatchewan, at Indian Head and Saskatoon, the spore counts showed a relation between south winds and an increased number of spores in the air, but in the first part of the summer the number of spores was lower than in the Red River Valley, and periods of south wind that brought a large number of spores to the Red River Valley did not always bring an appreciable number to Saskatchewan. In fact, the earliest spore showers usually did not extend so far west as Indian Head. In Alberta, spore showers were not very pronounced, and those that did occur usually took place in the latter part of July or in August, and did not regularly coincide with periods of south wind.

The reason for these circumstances appears to lie in the fact that south winds reaching Alberta and, to a lesser extent, western Saskatchewan must pass, respectively, over a mountainous area where relatively little grain is grown or over the semi-arid Great Plains region where stem rust is usually of little consequence, and hence abundant inoculum for transportation northward is lacking. This statement is apparently not true of the year 1938, for in all probability, as indicated earlier, a great deal of inoculum was brought into these two areas by south wind, because of the unusual westward extension of heavy stem-rust infection in the Mississippi Valley in that year. The spore-bearing winds come largely from the southeast and east, and, as will be shown a little later, the winds adverse to the introduction of spores into these two areas markedly predominate.

Frequency of South Winds in Relation to Stem-Rust Outbreaks

To ascertain whether or not any association exists between years in which south wind was of particularly frequent occurrence during the summer and years in which epidemics of stem rust developed in Western Canada, relevant data are given in Table 21 for eastern Manitoba, the region where the association would probably be most readily discernible, if such an association actually exists. This table gives the total number of hours of south wind (S.E., S., S.W.) at Winnipeg between June 12 and July 20 from 1921 to 1938, and the total number of days between those two dates, from 1916 to 1938, on which low and high air-pressure areas were so positioned as to bring a south wind of 12 or more hours duration to eastern Manitoba. It will be observed that the average number of hours of south wind in the heavy rust years exceeded that in the light rust years by about 25 hours, and the average number of days with south wind was greater by one in the former than in the latter class of years. The fact, however, that, in the medium rust years, the average number of hours and of days with south wind are greater than in the other two classes of years, seems to indicate that a day more or a day less of south wind is not of much conse-

TABLE 21.—TOTAL HOURS OF SOUTH WIND (SE., S., SW.) AT WINNIPEG, MAN., BETWEEN JUNE 12 AND JULY 20 FROM 1921 TO 1938, AND NUMBER OF DAYS IN WHICH LOW AND HIGH ATMOSPHERIC PRESSURE AREAS WERE IN SUCH A POSITION AS TO BRING A SOUTH WIND OF TWELVE HOURS OR MORE DURATION TO SOUTHERN MANITOBA BETWEEN THE SAME DATES FROM 1916 TO 1938, FOR YEARS IN WHICH STEM RUST WAS LIGHT, MEDIUM, AND HEAVY IN THE PROVINCE OF MANITOBA

Light			Medium			Heavy		
Year	Hours	Days	Year	Hours	Days	Year	Hours	Days
1917		18	1919		18	1916		15
1918		15	1921	447	23	1923	350	15
1920		13	1924	601	21	1927	460	19
1922	374	17	1925	428	19	1935	376	16
1926	289	11	1930	422	16	1938	420	19
1928	308	13	1937	378	14			
1929	465	22						
1931	394	16						
1932	337	14						
1933	446	19						
1934	387	18						
1936	388	17						
Total	3308	193		2276	111		1606	84
Mean	376.4	16.1		455.2	18.5		401.5	16.8

quence. Actually, it is not so much the duration or frequency of south wind that matters but the amount of inoculum that it introduces. The likelihood is that in every year the number of hours or of days of south wind during the critical period for stem-rust infection is great enough to introduce ample inoculum to initiate an epidemic, if weather conditions are favourable and stem rust is abundant in the northern Mississippi Valley.

Wind from Other Directions in Relation to Spore Introduction

The evidence just presented indicates clearly an association in Western Canada between the occurrence of southerly wind and the presence of a high concentration of stem-rust inoculum in the air. In regard to westerly winds, they pass over the Pacific Northwestern States and British Columbia, areas traversed by high mountain ranges that run in a general north-to-south direction. These mountains, no doubt, present a considerable barrier to the eastward dispersal of fungal spores, but probably not an insurmountable one. The ranges are broken by passes, and it is quite possible that spores produced in the valleys or plateaux of these areas may be carried by surface winds eastward through such passes, or even across the mountain ridges themselves. At any rate, spread of stem-rust inoculum in the opposite direction, from the Mississippi Valley into the Western Highlands, is known to occur in some years (67, 85). Furthermore, both the Pacific Northwestern States and British Columbia lie in the zone of westerly winds, in which the upper winds are prevailingly westerly. They are not retarded, as the surface winds are, by friction against the earth, and hence have usually a higher velocity than the surface winds. In mountain regions during summer, owing to the unequal heating

of the irregular land surface, strongly ascending air columns are commonly present. Spores carried up by these to higher levels would be carried eastward by the upper winds. Presumably, therefore, in spite of the mountain barriers, spores originating in these two areas west of the Rockies can be blown into Western Canada. As pointed out earlier, however, it is unlikely that any of the early inoculum or even any considerable amount of the later inoculum reaching Western Canada originates in these areas, although there is evidently the possibility that in occasional years a slight amount of the later arriving inoculum may do so.

Northerly winds play little or no part in the introduction of inoculum. They blow across a vast uncultivated area of even topography, and, were inoculum present in this area, could readily carry it into the cultivated area of Western Canada. As pointed out earlier, however, the growing season in the uncultivated area is later than in the cultivated area, and hence any inoculum arising on native grasses in the former area would be produced too late to have any influence on the course of stem-rust development in the latter area.

Easterly winds before reaching Manitoba, the most eastern portion of Western Canada, must pass over a territory several hundred miles wide, largely covered with forest or lake. In it, as mentioned earlier, the growing season is later than in Western Canada and cereal production is of comparatively little importance. The amount of stem-rust inoculum produced must be small, but there seems to be no good reason why some of what may be produced should not be carried by easterly winds into Western Canada, although this inoculum would arrive after stem rust became established in the latter area. East of this belt lie the main agricultural areas of Eastern Canada—eastern Ontario, Quebec, and the three Maritime Provinces—and the more northern Eastern States. The possibility of inoculum produced in these two areas being carried by winds to Western Canada seems, in general, to be rather slight.

The basis for this conclusion lies in the fact that, during the summer months, the air-pressure areas, as they pass eastward, are seldom if ever in a suitable relation or position to provide favourable winds for the purpose in question. As a rule, the high pressure areas pass south of the Great Lakes and most of the extensive low pressure areas pass over or north of these lakes, so that very rarely are the air-pressure areas in such a relation as to permit a flow of air from these two eastern areas into Western Canada. Furthermore, the movement of these pressure areas eastward is usually fairly rapid, and even were they temporarily in a suitable position for surface winds to carry spores westward, say from southern Ontario to Manitoba, it is doubtful if they would remain long enough in that position for the spores to reach their supposed destination. There is even less probability that spores could be carried westward by upper winds. The regions involved lie in the westerly wind zone, where the upper winds are prevailingly from the west. An examination of meteorological maps giving the direction of the upper winds in these eastern areas during the summer months—the only period in which aerial dissemination of stem-rust inoculum has any significance for Western Canada—shows clearly that during these months the upper winds blow largely in an eastward direction. Presumably in all the years under review the same general tendency has

prevailed. The conclusion, therefore, seems to be justified that little or none of stem-rust inoculum reaching Western Canada originates in these eastern parts of the continent.

Prevalence of Winds Favourable to Spore Introduction

With a view of determining whether or not the hours of wind favourable to the introduction of stem-rust spores into different parts of Western Canada were appreciably greater than usual in heavy rust years, the mean hours of favouring wind for epidemic years and for the whole period (1922 to 1938) for which data are available are given in Table 22 for five stations for the three summer months. At most of these stations wind-hour records were initiated in 1922, and hence data for 1916, an epidemic year, and the next five years are not included. In the table the hours of wind favourable to spore introduction are printed in bold face.

TABLE 22.—MEAN HOURS OF WIND FAVOURABLE TO THE INTRODUCTION OF STEM-RUST SPORES IN JUNE, JULY, AND AUGUST, FOR FOUR HEAVY-RUST YEARS (1923, 1927, 1935, AND 1938) AND FOR THE 17-YEAR PERIOD 1922-1938 AT FIVE STATIONS IN WESTERN CANADA

Wind direction	Month	Winnipeg		Qu'Appelle		Scott		Lethbridge		Lacombe	
		Heavy-rust years	17-year period	Heavy-rust years	17-year period	Heavy-rust years	17-year period	Heavy-rust years	17-year period	Heavy-rust years	17-year period
		hr.	hr.	hr.	hr.	hr.	hr.	hr.	hr.	hr.	hr.
East	June	55.2	58.8	61.7	59.2	93.3	86.4	91.5	57.0	56.5	40.0
	July	44.0	47.2	**44.7***	**58.0**	**80.0**	**81.2**	**73.7**	**53.6**	**76.5**	**64.6**
	August	51.5	56.3	**51.5**	**57.6**	**63.7**	**60.1**	**76.7**	**51.5**	**49.0**	**48.2**
Southeast	June	**130.5**	**118.4**	**124.5**	**112.4**	**139.6**	**115.9**	**45.5**	**64.1**	**125.7**	**117.7**
	July	**144.0**	**131.9**	**85.7**	**124.5**	**80.5**	**116.2**	**66.2**	**75.1**	**95.7**	**117.9**
	August	**129.7**	**135.5**	**107.2**	**117.2**	**82.2**	**115.0**	**61.2**	**68.1**	**79.7**	**90.2**
South	June	**92.2**	**86.3**	**94.7**	**78.5**	49.0	48.9	63.2	61.2	129.7	96.9
	July	**92.7**	**100.7**	**69.7**	**74.5**	62.0	65.0	65.7	60.1	114.0	128.5
	August	**97.5**	**102.1**	**98.7**	**81.6**	69.7	56.2	64.7	57.3	130.0	156.9
Southwest	June	**59.5**	**82.0**	84.7	105.4	54.2	77.7	96.0	153.5	86.0	88.8
	July	**72.5**	**76.5**	123.5	109.7	64.0	69.7	105.0	170.9	115.7	99.7
	August	**92.5**	**92.8**	112.2	128.6	88.0	74.3	124.2	165.0	122.5	107.0

* The figures in bold face indicate that at the respective stations the wind was favourable to the introduction of stem-rust spores.

Spore-bearing winds in the main can come only from four directions, namely, east, south-east, south, and south-west. As in June stem rust is usually only present in traces or is absent in Western Canada, and there is practically no likelihood of spores coming from more eastern areas, east wind during this month is not regarded as favourable to the introduction of spores in any part of Western Canada, or during the other two months in Manitoba. In July and August, however, owing to stem-rust development in Manitoba and eastern Saskatchewan, this wind becomes a spore-bearing one for more western parts. South-west wind is probably only of importance for Manitoba and possibly eastern Saskatchewan, as wind from that direction reaching western Saskatchewan and Alberta would largely

pass over territory in which there would be usually comparatively little stem rust. For a similar reason, as mentioned earlier, south wind reaching the two latter areas is probably of little importance in introducing spores, and hence for them is not regarded as a spore-bearing wind. Exceptionally, however, south wind may become of importance as a spore-bearing wind for these two areas, for, as has already been pointed out, it is probable that in 1938 south winds brought a considerable quantity of spores to western Saskatchewan and possibly also to Alberta. At any rate, the prevalence of stem rust in these two areas in a comparatively dry year would seem to indicate that an unusually large amount of inoculum must have been present.

It is evident from Table 22, that for heavy rust years the average number of hours of wind favouring the introduction of spores at the different stations are in some instances higher, in other instances lower, than the average number for the 17-year period. For example, the number of hours of southeast wind in June is slightly higher at Winnipeg, Qu'Appelle, Scott, and Lacombe, although lower at Lethbridge, for the heavy rust years; but in July the number is higher only at Winnipeg, and in August at none of the stations. Actually, in June, or the greater part of it, southeast winds have probably little significance for Manitoba or eastern Saskatchewan as far as the importation of spores is concerned, for such winds pass largely over a territory of forest and lake, and during most of that month stem rust is largely absent from any cereal-producing areas in that direction. In this connection, it may be remarked that when spore showers occur in June, their occurrence is associated with direct south wind. With regard to the other wind directions, a similar situation generally obtains. The average number of hours of south wind in June at Winnipeg and Qu'Appelle, for the heavy rust years, is slightly higher than the respective 17-year averages for those two points, although probably not sufficiently higher to have any significance, but the average is lower for the heavy rust years at Winnipeg in the other two months, and in July at Qu'Appelle. For the same two stations, the average number of hours of southwest wind in each of the three months (excepting August for eastern Saskatchewan) is less for the heavy rust years than for the average year. Broadly speaking, the data seem to support the evidence already given that epidemic years are not characterized by an increased frequency or duration of winds favourable to the introduction of stem-rust spores, and they are in general accord with Lambert's (113) conclusion in respect to the Mississippi Valley, namely, that no association exists between years in which stem-rust epidemics occur and years in which conditions seem most favourable for spores to be blown up from the south.

Factors Contributory to Regional Differences in Stem-Rust Severity

Reference has already been made to the fact that Manitoba and eastern Saskatchewan are invariably more severely affected by stem rust than are western Saskatchewan and Alberta (*cf.* Figure 1). In the latter region, the comparative freedom from severe stem-rust damage is not attributable to resistance in the crops, as susceptible varieties are still

almost exclusively grown. The geographical position of the two regions and the intimately related meteorological conditions seem to account satisfactorily for the marked differences in the amount of infection between the two regions. As mentioned previously, the more easterly region lies directly north of the Mississippi Valley and is directly exposed during periods of south wind to the introduction of stem-rust spores from that area, where severe outbreaks of the disease periodically occur. The more westerly region, on the other hand, lies north of a mountainous territory in which grain-growing is somewhat more limited and stem rust relatively unimportant, so that this region is less directly exposed to heavy spore invasions from the south. It should be mentioned, however, that for this more westerly region (western Saskatchewan and Alberta), an additional source of inoculum is the more easterly region (Manitoba and eastern Saskatchewan), especially in seasons when a stem rust is prevalent in the latter; but this source seldom becomes of importance until the middle of July, and in some years even later.

Winds Favouring or Opposing Spore Introduction

The advantage of the more westerly over the more easterly region in respect to freedom from stem rust is shown in the lesser number of hours of wind favourable to the introduction of rust spores. Table 23 gives the mean number of hours of wind favouring, and opposing, the introduction of spores at six stations in Western Canada for June, July, and August, from 1922 to 1938. Winnipeg may be taken to represent eastern Manitoba; Qu'Appelle, eastern Saskatchewan; Scott, western Saskatchewan; and Lethbridge, Calgary, and Edmonton, the southern, central, and northern parts of Alberta, respectively. Winds favourable to the introduction of spores in eastern Manitoba are from a southerly direction (SE., S., SW.), whereas such winds in Alberta are easterly (E., SE.); unfavourable or opposing winds in the former are northerly (NE., N., NW.), in the latter, northerly and westerly (N., NW., W., SW.). Between the sector favouring and that opposing spore introduction are two opposite sectors, referred to as varying, in which the winds may perhaps at one time favour, at another time oppose the introduction of spores.

It will be seen from Table 23 that, during the 17-year period 1922 to 1938, the mean number of hours of favouring wind per month at Winnipeg and Qu'Appelle, the two more eastern stations, are not greatly less than the mean number of hours of opposing winds. In fact, at Winnipeg, in July and August, the hours of favouring wind exceed those of opposing wind. At the stations in the more westerly region (Scott, Lethbridge, Calgary, and Edmonton), the mean number of hours of favouring wind are much less than at the two more easterly stations, and are from two to three times less than of opposing wind. Spores therefore originating, for instance, in the Upper Mississippi Valley, have not only much farther to travel to reach the more westerly region than to reach the more easterly one, but have much fewer hours of favouring wind by which to make the journey.

TABLE 23.—MEAN HOURS OF WIND PER MONTH FAVOURING OR OPPOSING THE INTRODUCTION OF WIND-BORNE SPORES FOR JUNE, JULY, AND AUGUST DURING THE 17-YEAR PERIOD 1922-1938, AT SIX STATIONS IN WESTERN CANADA, TOGETHER WITH THE MEAN HOURS OF WIND FROM OTHER DIRECTIONS

Station	Classes of wind	Mean hours per month		
		June	July	August
Winnipeg, Man.	Favouring (S.E., S., S.W.)	286.7	309.1	330.4
	Opposing (N.E., N., N.W.)	302.7	296.3	266.1
	Varying (E., W.)	127.8	132.5	144.8
Qu'Appelle, Sask.	Favouring (E., S.E., S.)	250.1	257.0	256.4
	Opposing (N., N.W., W.)	281.5	316.5	304.1
	Varying (N.E., S.W.)	179.6	161.8	176.1
Scott, Sask.	Favouring (E., S.E.)	202.3	197.4	175.1
	Opposing (N., N.W., W., S.W.)	388.3	409.1	440.9
	Varying (N.E., S.)	127.9	135.5	125.9
Lethbridge, Alta.	Favouring (E., S.E.)	121.1	128.7	119.6
	Opposing (N., N.W., W., S.W.)	469.2	460.2	467.6
	Varying (N.E., S.)	119.3	126.0	122.6
Lacombe, Alta.	Favouring (E., S.E.)	157.7	182.5	138.4
	Opposing (N., N.W., W., S.W.)	373.8	356.3	372.4
	Varying (N.E., S.)	166.3	184.7	208.7
Calgary, Alta.	Favouring (S., S.E.)	158.3	167.2	139.4
	Opposing (N., N.W., W., S.W.)	430.1	433.8	470.4
	Varying (N.E., S.)	108.0	112.1	117.0

Differences in Rainfall

With regard to rainfall in Western Canada, it has been shown that seasons of medium and heavy rust infection have a greater rainfall than seasons in which infection is light. From Table 9, it will be seen that the average rainfall for the spring and summer months in the two Manitoba divisions is greater than in the eastern Saskatchewan division (Qu'Appelle River) and still greater than in each of the two western Saskatchewan divisions and the north-central one (Saskatchewan Forks). In the Alberta divisions, however, the rainfall shows an increase over that of western Saskatchewan, the increase being largely due to the higher rainfall in the western portion of those divisions. This general trend in the rainfall of Western Canada is represented in Figure 12, which is, for the most part, an adaptation of a precipitation map issued by the Research Department of the Searle Grain Company Limited, Winnipeg, and represents the long-time average precipitation of the period April 1 to July 31 of each year combined with the average annual precipitation of the period August 1 to October 31 of the preceding year. From this figure, it will be seen that the precipitation for the months indicated is highest in southern Manitoba and in the more elevated area just east of the Rocky Mountains. The area of least precipitation spreads out on either side of the Saskatchewan-Alberta boundary. In occasional years, there may be wide deviations from the long-time average in certain areas, as happened, for example, in the South Saskatchewan River division (southwestern Saskatchewan) in 1916,

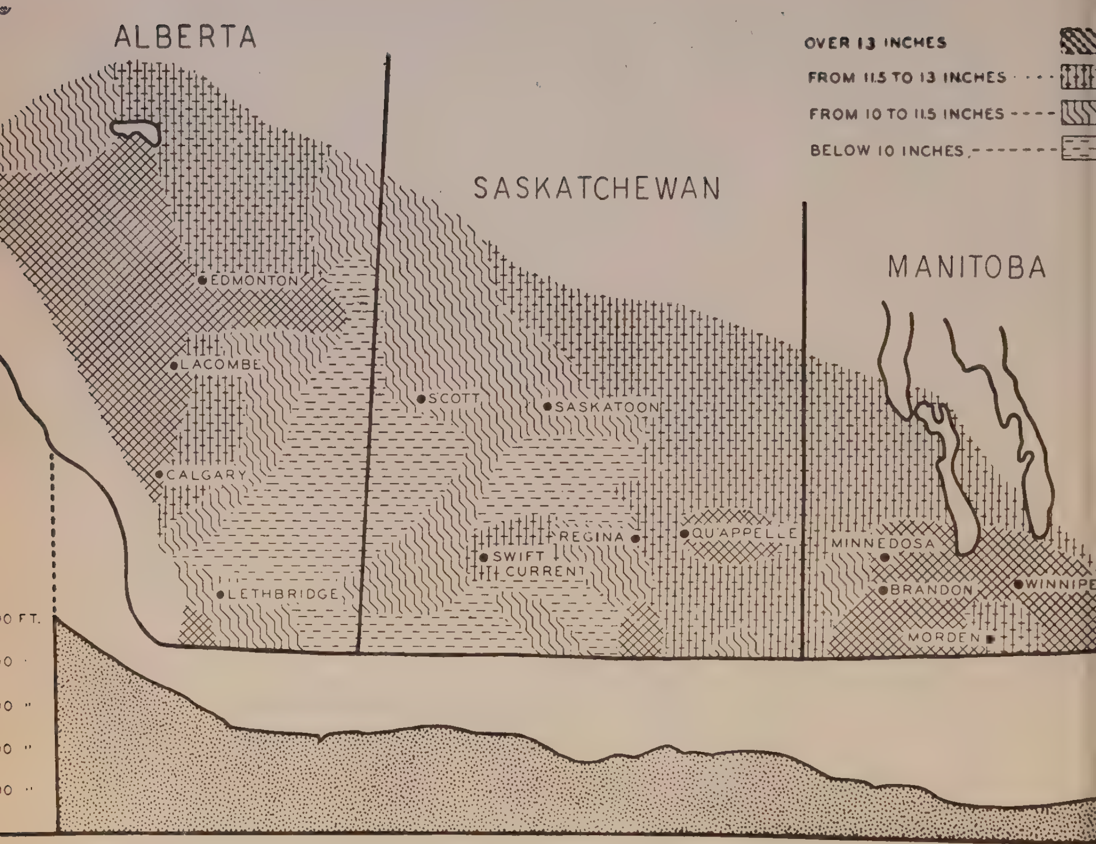

FIGURE 12. Map of Western Canada showing the average long-time precipitation (in inches) during the periods August-October of one year and April-July of the following year. The lower portion of the figure indicates the altitude (in feet) of points along a line passing through Winnipeg, Brandon, Qu'Appelle, Regina, Swift Current, and Calgary.

1923, and 1927, three epidemic years in which the spring and summer rainfall was 83, 54, and 70%, respectively, higher than the 23-year average. The lower rainfall in western Saskatchewan and eastern Alberta tends very probably to afford this more westerly region a certain amount of protection against infestations of stem rust, although in passing it may be mentioned that in this region in 1938, a year in which stem rust did considerable damage, the spring and summer rainfall was an inch or more below average. In this region, however, temperatures are lower, particularly at nights, than in the more easterly region, and for this reason the effectiveness of the moisture is somewhat greater, a circumstance which perhaps in some measure tends to compensate for the lower precipitation. Nevertheless, the fact that in four out of the five years in which stem rust was prevalent in this westerly region the rainfall was considerably above average, indicates that the lower rainfall in this region probably hinders the westward advance of the disease.

Differences in Temperature

Earlier in this paper, it was pointed out that, in the more westerly meteorological areas of Western Canada, summer temperatures are on the average lower than in the eastern divisions. Similarly, temperatures in northern districts tend to be somewhat lower than in southern districts. For instance, the mean temperature for the 3-month period, June to August, in the Red River (Manitoba) division is 65.2° F. and in the Bow River (Alberta) division it is 61.3° F., while in the North Saskatchewan (Alberta) division it is 58.7° F. The temperature, of course, decreases as the altitude increases. It will be seen from Figure 12 that the land surface rises from east to west. Winnipeg, for example, has an elevation of 772 feet and Calgary of 3,438 feet. For this western region, as already mentioned, August is the critical month in respect to stem rust. When the temperature falls below 60° F., stem-rust development is appreciably retarded, and even infection may be impeded if the fall is pronounced. For the 23-year period under review, the average temperatures for August in the five more westerly meteorological divisions are as follows: in Saskatchewan—South Saskatchewan River, 63.0°, and North Saskatchewan River, 60.3° F.; in Alberta—Bow River, 61.4°, Red Deer River, 59.1°, and North Saskatchewan River, 58.3° F. It is thus seen that the average temperature for August in three of these divisions is below 61° F., a temperature below which Stakman and Lambert (207) found that no epidemics had occurred in the Upper Mississippi Valley. In another division, it is only slightly higher. In spite, however, of the relatively cool temperature in August in this more westerly region, stem rust is prevalent in occasional years and causes some damage. Nevertheless, there is little doubt that the disease is held somewhat in check by August temperatures. The same is true of the Saskatchewan Forks division, in north-central Saskatchewan, where the average temperature for August is 61.5° F. On the other hand, it is evident from Table 15 that the seasons in which stem rust was most prevalent in these meteorological divisions were no warmer generally than the average season.

TIME OF SEEDING AND OF HARVESTING IN RELATION TO OCCURRENCE OF STEM-RUST EPIDEMICS

It is generally accepted that the time of seeding and of harvesting a crop usually has an important bearing on the amount of stem-rust infection that develops in it. Under ordinary growing conditions in any given locality, a variety of wheat or of one of the other cereals ripens within approximately the same number of days from the time it is sown. If seeding is early or late, harvesting is usually expected to be correspondingly early or late. It has long been known that crops seeded early have a better chance than those seeded late of escaping stem-rust damage. Tull (219) recognized this fact more than two centuries ago, even though he was unaware of the true nature of the disease. Following the severe outbreak of the disease in Europe in 1804, Banks (11) stressed the importance of early crop maturity in preventing rust losses. In more recent times, it has been the experience of many investigators (46, 52, 59, 94, 129, 177, 211, and others) to find that early sown crops are usually lightly affected by stem rust. The growing of early-maturing varieties, likewise tends to

prevent severe losses from the disease (5, 58, 118, 142, 189, 211). On the other hand, late sown crops frequently suffer severe rust damage, as likewise commonly do late-maturing varieties (9, 34, 46, 52, 65, 67, 69, 89, 100, 123, 128, 195). Freeman and Johnson (67) point out that the critical period for infection in any given locality is a 10-day period about heading time, and that if for any reason this period is extended, the amount of infection is increased. Peltier (157) claims that an extended fruiting period (from heading to ripening) is one of the important factors favouring the development of an epidemic. In general, it may be said that when the period of exposure to inoculum is lengthened through any cause, the danger of heavy infection developing is increased.

As has been widely recognized, the explanation of the lighter infection on early ripening crops lies largely in the fact that when the disease appears they are farther advanced toward maturity than are the later ripening crops, and hence the disease is present on them a shorter time and cannot, therefore, interfere to so great an extent with their development. Besides, as the growing season progresses, the severity of the attack tends to increase, and hence the early grain, by ripening early, escapes the maximum amount of infection. Late sown crops, on the other hand, are still green and in a susceptible condition when inoculum is present in greatest abundance, and are, therefore, exposed to the heaviest possible infestation. On account of the cooler weather prevailing in the autumn in north temperate regions, such as Western Canada, the fruiting period of late sown crops is considerably prolonged and hence their exposure to infection is still further increased.

As a means of avoiding loss from stem rust, early seeding has been recommended for many years in Western Canada. This recommendation was based on experience and was made years before the source of inoculum that initiates stem rust in this region was investigated. Observation had shown that the earliest ripening fields usually escaped serious rust injury. Why this was the case is now apparent. Wind-borne inoculum undoubtedly has always been largely responsible for the initiation of stem-rust infection in this region. When once infection was established, the multiplication of inoculum, locally, proceeded with greater or less rapidity, depending on the number of initial infections and the favourableness of weather conditions. Concurrently with this local multiplication of inoculum, ever increasing amounts of inoculum were blown in from infected areas to the south, until harvesting there was largely completed. The longer the crops remained green after infection appeared, the longer was there the opportunity for new infections to occur and the multiplication of inoculum to take place.

There is no doubt that in any particular year if the varieties grown are susceptible to stem rust, the fields to ripen earliest are the ones least damaged by the disease, nor is there doubt that a prolongation of the period between heading and ripening of the crop gives opportunity for increased infection until maximum infection is established. The question considered here is whether or not in Western Canada seasons in which seeding or harvesting, or both, were early are associated with light rust years, and those in which one or both of these operations were delayed are associated with heavy rust years; and whether or not in heavy rust years the "fruiting period" of the grain was of more than average length.

A good deal of diversity occurs from year to year in the dates on which seeding and harvesting operations usually become general in Western Canada, the dates for each of these operations being from one to two weeks or more earlier in the southern parts of this area than in the northern parts. Table 24 gives for years of light, medium, and heavy stem-rust infection between 1916 and 1938, the dates on which wheat seeding and harvesting began generally in Manitoba and in eastern Saskatchewan, excepting in the most northerly parts. The dates for Manitoba have been taken from

TABLE 24.—DATES ON WHICH SEEDING AND HARVESTING OF WHEAT BEGAN GENERALLY IN MANITOBA AND EASTERN SASKATCHEWAN IN YEARS WHEN STEM-RUST INFECTION WAS LIGHT, MEDIUM, AND HEAVY IN THOSE AREAS BETWEEN 1916 AND 1938

Light			Medium			Heavy		
Year	Seeding	Harvesting	Year	Seeding	Harvesting	Year	Seeding	Harvesting
				Manitoba				
1917	Apr. 25	Aug. 16	1919	Apr. 25	Aug. 1	1916	May 1	Aug. 12
1918	Apr. 8	Aug. 18	1921	Apr. 28	Aug. 1	1923	May 5	Aug. 8
1920	May 3	Aug. 10	1924	May 5	Aug. 23	1927	May 5	Aug. 22
1922	Apr. 22	Aug. 5	1925	Apr. 15	Aug. 10	1935	Apr. 27	Aug. 8
1926	Apr. 14	Aug. 9	1930	Apr. 15	Aug. 5	1938	Apr. 12	July 30
1928	Apr. 25	Aug. 16	1937	Apr. 26	Aug. 4			
1929	Apr. 23	Aug. 8						
1931	Apr. 15	Aug. 5						
1932	Apr. 19	Aug. 1						
1933	Apr. 26	Aug. 1						
1934	Apr. 21	Aug. 3						
1936	Apr. 29	July 24						
Average	Apr. 22	Aug. 7		Apr. 23	Aug. 6		Apr. 28	Aug. 10

23-year average: Seeding, April 24; Harvesting, August 7

Eastern Saskatchewan

Year	Seeding	Harvesting	Year	Seeding	Harvesting	Year	Seeding	Harvesting
1917	May 6	Aug. 21	1919	Apr. 27	Aug. 2	1916	Apr. 24	Aug. 23
1918	Apr. 13	Aug. 19	1921	Apr. 26	Aug. 16	1923	May 4	Aug. 21
1920	May 6	Aug. 29	1925	Apr. 22	Aug. 18	1927	May 5	Aug. 29
1922	May 4	Aug. 18	1930	Apr. 18	Aug. 13	1935	Apr. 23	Aug. 11
1924	Apr. 29	Sept. 3				1938	Apr. 30	Aug. 10
1926	Apr. 19	Aug. 18						
1928	May 2	Aug. 25						
1929	Apr. 22	Aug. 17						
1931	Apr. 11	Aug. 11						
1932	Apr. 15	Aug. 11						
1933	Apr. 25	Aug. 4						
1934	Apr. 18	Aug. 12						
1936	Apr. 27	Aug. 2						
1937	Apr. 18	Aug. 3						
Average	Apr. 24	Aug. 16		Apr. 23	Aug. 12		Apr. 29	Aug. 19

23-year average: Seeding, April 25; Harvesting, August 16

Crop Bulletins published annually by the Manitoba Department of Agriculture, with the exception of those for harvesting in 1916 and 1917, which have been kindly furnished by the Experimental Farm, Brandon, Manitoba; those for Saskatchewan, from the Annual Reports of the Saskatchewan Department of Agriculture. In the areas indicated, the bulk of the wheat crop would usually be sown or harvested each year within two weeks of the respective dates given in Table 24. During the years under review, Marquis was the variety of wheat principally grown. It is quite susceptible to the races of stem rust commonly present in Western Canada, and on an average matures in 106 days in Manitoba but requires about a week longer to mature in Saskatchewan.

According to the data given in Table 24, the average date on which seeding of wheat became general in Manitoba during the 23 years under review is April 24, and for harvesting, August 7, an interval of 106 days; in Saskatchewan the date for seeding is April 25 and for harvesting, August 16, an interval of 114 days. In Manitoba, the average date in the heavy rust years for seeding is 4 days, and for harvesting 3 days later than for the whole period; thus the average length of time from seeding to harvesting in the heavy rust years is 1 day less than the 23-year average. In the light rust years, harvesting was on the same day as, and seeding 2 days earlier than for the whole period, thus making the period from seeding to harvest 2 days longer than the average for the 23 years. In other words, the average time from seeding to harvest in the heavy rust years was 3 days less than in the light rust years. In only one epidemic year (1927) did weather conditions delay markedly the maturing of the crop. In 1923, the time between seeding and harvest was surprisingly short, only 88 days. There is, however, the possibility that in the heavy rust years harvesting may have been begun slightly before the crop was fully matured, as there was a general belief among farmers that by cutting the crop "on the green side" less damage from the disease would result. This early commencement of harvesting in the heavy rust years, however, would not have probably reduced the period between seeding and harvesting by more than 2 or 3 days at most, so that ripening in the heavy rust years would likely have occurred within about the same number of days from seeding as was required in the light rust years.

As already indicated, the average time from seeding to harvest in Saskatchewan is about a week longer than in Manitoba. This difference is largely due to the somewhat higher elevation of eastern Saskatchewan, and the consequently cooler climate. On the average, seeding in the heavy rust years is 5 days later than in the light rust years, but harvesting is only 3 days later, so that actually the time between seeding and harvest in the heavy rust years is 2 days less than in the light rust years, and 1 day less than the 23-year average. Here, too, the early cutting of rusted crop may account for the shorter period between seeding and harvest in the heavy rust years. It may, therefore, he concluded that, on an average in Manitoba and eastern Saskatchewan, there was little or no difference between the heavy and the light rust years in respect to the length of time needed for the wheat crop to mature.

As seeding was 4 or 5 days later than average in the heavy rust years, it would be expected that, other things being equal, the crop in such years

would have been somewhat less advanced when stem-rust infection appeared than it was in other years, provided the infection appeared at about the average time. As shown in Table 25, the wheat crop in Manitoba was always in head or heading before stem rust became lightly prevalent in that province. In 1923, 1935, and 1938, heavy rust years, a general light infection occurred synchronously with heading in eastern Manitoba and rapidly became intensified. The same was true of 1937, a year of moderately heavy rust in most of Manitoba but of severe infection in the south-central portion. A light general infection occurred also at heading time in 1929 and 1936, two light rust years, but, in these two years, there was not a rapid subsequent increase of infection. In other years, a light general infection did not appear until several days or longer after the crop came into head, and in most of these years the intensification of the infection was less rapid than in 1923, 1935, and 1938. In these three epidemic years, the crop was undoubtedly less far advanced when infection became severe than it was in the other years, and hence heavy infection was longer present on the crop. The same observations apply in these years to western Manitoba, except that in 1938 heading was practically completed before a light general infection became prevalent. The wheat crop in this area was thus farther advanced when a light general infection developed than it was in eastern Manitoba.

Unforunately, consideration could not be given in this discussion to the years 1916 to 1922, as the data concerning the development of the disease and of the crop in those years are not sufficiently complete to warrant their being used as a basis for deductions. For the same reason, discussion dealing with eastern Saskatchewan is omitted. There is little doubt, however, that had the data been available for study the same general pattern found for Manitoba from 1923 to 1938 would apply, namely, that in the heavy rust years the period from seeding to harvest was about of average length, that a light general infection did not occur until the crop was heading or in head, and that the light general infection passed rapidly into severe infection. It would seem, therefore, that in Western Canada, as far as the time factor is concerned in the development of stem-rust epidemics, the crux of the situation lies in the early establishment of a light general infection and its rapid transition into a heavy infection. Only in one heavy rust year, 1927, was the development of an epidemic associated with a marked prolongation of the fruiting period of the crop. As has been already pointed out, however, a prolonging of the fruiting period is undoubtedly of importance every year in the establishment of heavy infection on late crops.

CROP MATURITY IN RELATION TO EARLY INFECTION

It was mentioned earlier that infections rarely or never appear in a district of Western Canada until the crop or a considerable part of it in that district has headed or is at least in the process of heading. In some other parts of the world the appearance of stem rust in the field seems to coincide with or follow the heading of the grain crop. Peltier (157) mentions that in Nebraska, over a period of 10 years, stem rust was never found in the spring on winter wheat before the crop had reached the very late boot or early heading stage, a fact which he attributes to lack of

inoculum and to unsuitable weather conditions. Traces of it, however, do occasionally occur in late autumn on seedling plants of this crop (158). Verwoerd (223) states that in the Cape province of the Union of South Africa, no infection usually appears before the wheat is in head. According to Shitikova-Roussakova (183), infection in the Amur Region in Eastern Asia is usually first seen in the field at the time of heading and flowering of the wheat. D'Oliveira (53) states that in Portugal stem rust appears in the crop during or after heading. In Kenya, East Africa, Thorold (217) relates that stem rust does not usually appear until the crop is tillering or heading, and Dawson (50), that it nearly always appears late, generally after flowering time.

The freedom, or comparative freedom, from infection of cereals prior to heading has been attributed by some investigators to the greater resistance of the less mature plants. In a study of the relation of the time of seeding and stage of plant development to rust development, Bolley (21) sowed 8 varieties of oats at 14 different dates from April 5 and June 23 in 1895 and 1896, and concluded from his tests that all varieties were comparatively resistant to the rusts (stem rust and crown rust) until a period of their growth approaching the flowering time. Later, he (22) states that, with some varieties of wheat and oats, the tissue must attain a certain degree of maturity before it is congenial to the rust. After mentioning that soft succulent wheat stems are more open to rust attack than others, Bolley and Pritchard (24) remark that every variety is "more open to attack by rust just at the period following heading time to the point of full blossom stage." Freeman and Johnson (67) found that plants inoculated between heading and full bloom were more severely rusted than plants inoculated before or after this period. They suggest that at that stage there may be a particular physiological weakness due to rapid growth and abundant elaboration of starch that might increase the susceptibility of the grain.

As a deduction from the results of their trials of wheat varieties for rust resistance, Jenkin and Sampson (101) drew the conclusion that there appeared to be one or more periods during the maturity of the plant when it is most susceptible to rust. In a report on the behaviour of certain wheats to rust attack in the vicinity of Paris in 1923 and 1924, Foex Gaudineau, and Guyot (62) relate that Goldendrop, a winter wheat, was sown in the autumn and in the spring. At the first of August, the spring sown plots, still in the tuft stage, were surrounded with plants heavily infected with stem rust, but although some leaf-rust pustules were present in the plots, there were no stem-rust pustules. The autumn sown plots, however, bore a moderate infection of stem rust. This circumstance seemed to indicate that the stage of growth had some influence on the development of the rust. Careful observation of the development of stem rust on 1,290 pure lines of wheat, particularly on lines of Strube, led Roussakov and Pantchenko (174) to the conception of immunity in time, in contradistinction to absolute immunity, that is to say, immunity only until the setting in of a certain stage in the development of the host plant, the stage in some lines being that of ear formation, in others the milk stage, and in still others the last few days of vegetation. Levine (118) states that, although his results might be open to a different interpretation,

there seems to be "sufficient observational evidence to indicate that the susceptibility of plants does depend to a considerable extent on their stage of development. They seem to be quite susceptible in the seedling stage and again at about the heading-out stage. In the jointing stage the plants show more resistance."

Gassner (71, 72, 74) concluded from his experiments in South America and Germany that wheat plants when young (up to the heading stage) are more resistant to stem rust than when older, although resistance again appears just prior to ripening. This view seems to be held by Cornelli (42) who states that, near Perugia, Italy, a strip of Mentana wheat growing between two strips of the Gentil rosso variety was attacked by stem rust while the latter variety showed no indication of infection. He points out that the Mentana variety is earlier but more rust resistant than the Gentil rosso variety, and he attributes the occurrence on the former and its absence on the latter (the more susceptible variety) to a difference in plant maturity. From experiments in 1927 and 1928 on the effect of the date of seeding on the amount of rust infection, Brega (26) found that early sowing appeared to conduce to early infection, that is to say, infection appeared earliest on the earliest sown plots (these being presumably the farthest advanced in degree of maturity).

On the other hand, Stakman and Piemeisel (212) found that cereals are usually susceptible at any age up to ripening time, and Stakman and Levine (208), that oat seedlings up to 35 days of age are quite susceptible. Peltier (156) states that in his experience susceptibility to stem rust was greater in the seedling stage of cereals than in later stages of growth. Goulden, Newton, and Brown (78) proved that certain wheat varieties that are susceptible in the seedling stage become highly resistant after heading, that is to say, they become resistant with age. Newton and Brown (147) have shown that, in wheat varieties possessing mature-plant resistance, the younger tissue is susceptible to stem rust while the older tissue of the same plants is resistant. Hart and Forbes (82) state that wheat plants in southern Minnesota have been observed badly rusted in all stages of growth prior to heading of the plants. Lambert (113) points out that, in the spring wheat area (Upper Mississippi Valley), stem rust spreads from barberry to grasses and grains during the last two weeks of May. As at that time of year, spring wheat in that region is not yet in head, the infection must occur on plants in younger stages of development. Furthermore, stem rust usually overwinters on autumn sown crops. It is also a well-known fact that susceptible cereal plants can be successfully inoculated at all stages of growth between emergence and maturity. In experimental plots at Winnipeg, a limited amount of infection has appeared almost every year on susceptible varieties of wheat as a result of artificial inoculation—the distribution of inoculum produced under greenhouse conditions—before such varieties came into head. There seems to be no doubt, therefore, that crops in pre-heading stages may become infected to a greater or less extent by stem rust.

Time of Heading in Relation to Early Rust Appearance

The question, therefore, arises as to what extent, if any, the appearance of field infections in Western Canada is dependent on the stage of crop

maturity. Table 25 gives for eastern and western Manitoba the dates on which heading of wheat became general each year from 1923 to 1938, together with the dates on which stem-rust infections were first detected in the field and the dates on which a light general primary infection appeared. The dates given for heading becoming general and for the appearance of a light general infection represent, respectively, the periods in which the bulk of the wheat crop in southern and central Manitoba came into head and in which approximately 1% of the plants bore a trace of primary infection. Data relative to the other two provinces, Saskatchewan and Alberta, are not included in this table owing to their incompleteness, but the data that are available for these two provinces are entirely in agreement with the observations made in Manitoba, namely, that stem-rust infections appear on crops at or after heading.

TABLE 25.—DATES ON WHICH HEADING OF WHEAT BECAME GENERAL, ON WHICH STEM-RUST INFECTIONS WERE FIRST DETECTED, AND ON WHICH A LIGHT PRIMARY INFECTION BECAME GENERAL IN EASTERN AND WESTERN MANITOBA FROM 1923 TO 1938

—	Eastern Manitoba			Western Manitoba		
	Heading of wheat	Earliest stem-rust infection	Appearance of light general infection	Heading of wheat	Earliest stem-rust infection	Appearance of light general infection
1923	July 3–10	July 5	July 5–12	July 4–11	July 6	July 8–15
1924	July 12–19	July 7	July 12–19	July 14–21	July 18	July 18–25
1925	July 7–14	June 23	July 10–17	July 9–16	July 12	July 13–20
1926	July 3–10	July 2	July 8–15	June 28–July 5	July 16	July 18–25
1927*	July 8–20	July 6†	July 12–19	July 4–11	July 15	July 17–24
1928	July 7–14	July 9	July 20–27	July 3–10	July 20	July 23–30
1929	July 3–10	July 3	July 3–10	July 5–12	July 3	July 4–11
1930	July 2– 9	June 26	July 6–13	July 1– 8	July 5	July 9–16
1931	June 29–July 6	July 5	July 7–14	July 1– 8	July 12	July 18–25
1932	June 20–27	June 20	July 1– 8	June 19–26	July 7	July 10–17
1933	June 28–July 5	June 28	July 10–17	June 25–July 2	July 14	July 15–22
1934	July 5–12	July 5	July 9–16	July 1– 8	July 15	July 16–27
1935	July 5–12	July 2	July 3–10	July 4–11	July 3	July 3–10
1936	June 27–July 4	June 26	June 27–July 4	June 30–July 7	July 1	July 1– 8
1937	July 5–12	July 1	July 6–13	June 28–July 5	June 28	June 29–July 6
1938	June 26–July 3	June 22	June 27–July 4	June 22–29	June 22	June 28–July 5

* An unusually wet growing season caused marked variation in the stage of crop maturity from field to field, hence the period of heading was unduly prolonged.
† Infection first appeared on winter wheat plots at Winnipeg.

A comparison of the dates on which heading of wheat became general and on which a light general infection appeared in eastern Manitoba, shows that in several years—1923, 1924, 1929, 1935, 1936, 1937, and 1938—the dates were synchronous or nearly so. In all of the other years, the heading of wheat preceded, by a few days to a week or more, the appearance of a light general infection. Only in 1935 did a light general infection appear before heading was well underway. In this year infections began to appear in many fields on the uppermost leaves when the heads were only partly emerged from the sheaths. Infections on the stems began to appear 3 or 4 days later. In western Manitoba, there is close agreement of dates

in 1929, 1935, 1936, and 1937, but in the other years, heading of wheat always preceded the appearance of a light general infection by a less or great number of days. It may, therefore, be said that in every year wheat in Manitoba had headed or was heading by the time scattered primary infections appeared in this crop. This fact does not necessarily indicate that the date of heading influenced the time when a light infection became general. Indeed, the variation in the length of interval between the time of heading and of light general infection from year to year would indicate that some other factor or factors determined the time that light infection became general. As a matter of fact, the only years in which the appearance of a light general infection could have been delayed by the maturity of the crop would be those years in which light general infection synchronized with the heading of the crop, as obviously, after the crop had headed, immaturity of the crop could not be held responsible for any delay thereafter in the appearance of the rust. Consideration may, therefore, be given to those years in which the appearance of a light general infection synchronized with the heading of the crop, in order to ascertain to what extent in these years the time that a light infection became general was influenced by the arrival of inoculum and by weather conditions.

Time of Appearance of a Light General Infection in Relation to Arrival of Inoculum and to Weather Condition Prior to Heading of Crop

Between 1923 and 1938, as mentioned above, the appearance of a light general infection synchronized with the heading of the wheat crop in 1923, 1924, 1929, 1935, 1936, 1937, and 1938. Of these seven years, two, 1923 and 1924, must be excluded from consideration, as, for them, data relating to the time of arrival and the amount of inoculum are lacking. In 1935, practically no spores were detected in the atmosphere before June 23, but a heavy spore shower occurred on June 24 and 25. Rain fell on June 24, 25, and 26, amounting to 0.56 inches, a trace, and 0.18 inches, respectively. Much infection undoubtedly occurred at this time. Between June 24 and July 5, the average daily temperature was 69.1° F., with an average daily maximum of 76.9° and average daily minimum of 61.3° F. Infections began to appear at Winnipeg on July 2, and by July 5 a light general infection was beginning to become established, which increased unusually rapidly to a moderately heavy infection by July 12. With such temperature conditions from June 24 to July 5, the time required for a light general infection too appear—if, as supposed, much infection occurred on June 24, 25 and 26—seems rather long (10 to 12 days), but probably not unduly long in view of the persistent heavy cloudiness prevailing during much of that period. Stakman and Piemeisel (212) claim that in cloudy weather the incubation period may be prolonged by a week. The more extended but lighter spore showers, from June 28 to July 5, apparently were responsible for the very rapid transition from light to moderately heavy infection. There is probably, therefore, little ground for supposing that in this year the time of rust appearance was influenced by the developmental stage of the crop.

To provide a basis for a discussion with respect to the remaining four years, data on weather conditions and the time of arrival and the relative numbers of urediospores present in the air are given in Table 26 for a period of 18 days prior to the appearance of a light general infection on wheat in the fields of eastern Manitoba. The probability of dew formation at night was arrived at by consultation of Smithsonian Meteorological Tables, mentioned in connection with the discussion of dew in relation to outbreaks of stem rust. Sufficient data are presented to indicate fairly clearly the kind of weather that prevailed during the period involved in each of the four years.

In 1929, a heavy spore shower occurred on June 16 and 17, the number of spores intercepted by the slides exposed at Winnipeg being 133 and 193, respectively. Rain fell on June 17 and probably there was deposition of dew on the preceding night. No more spores, except one on June 27, were detected by the slides until July 3, the day on which the first pustules appeared and a light general infection began to develop. During the interval from June 17 to July 3, the mean temperature was 62.3°, the mean daily maximum 73.6°, the mean daily minimum 52.1° F., the range being from 87° to 41° F. The weather was generally cloudy and damp with a trace or more of rain on 11 of the 17 days. On the supposition that infections occurred on June 16 and 17, a period of 16 days was, therefore, required for the development of the earliest appearing pustules. The question, therefore, to be decided is whether or not, under the temperature and light conditions that prevailed, the organism actually required that length of time for pustule development.

To this question perhaps no categorical answer can be given, but some indication of the length of time required may be gained from greenhouse experiments in which the temperature fluctuated within a more or less comparable range. For instance, Newton and Johnson[9] found that, in greenhouse experiments, inoculations made on wheat seedlings on April 28 resulted in full pustule development by May 16, a period of 18 days, during which the mean temperature was 62.6°, the mean daily maximum 74.5°, the mean daily minimum 51.2°, and the range from 85° to 42° F. While this experiment, and the ones mentioned later were in progress, the weather at Winnipeg was generally cloudy, a condition that tended to retard rust development. In view of the very considerable cloudiness from June 17 to July 3, 1929, there is a good possibility that stem rust would have required upwards of 16 days for development.

In 1936, the first definite spore shower occurred on June 12 and 13, and the first pustules appeared in the field on June 26. This spore shower was light in comparison with those of 1929 and 1935. Some infection may have occurred on June 12, 13, and 14, although conditions were perhaps not very favourable for that process. A trace of rain fell on the first two days, but, probably owing to the wind velocity, the plants soon dried and no dew was deposited at night. Dew probably was present in the third night, but the low temperature (min. 43° F.) likely inhibited any considerable amount of infection. On June 15 and 16, however, there was rain and the

[9] Unpublished data of Dr. Margaret Newton and Dr. Thorvaldur Johnson, Dominion Laboratory of Plant Pathology, Winnipeg, Manitoba.

sky was completely overcast, so that it is probable infection occurred on these days, particularly during the daylight hours of June 15. No further spores were detected until June 25 and no more rain fell until June 26, although dew likely occurred on several nights of this interval. There is a strong probability that the rust pustules that appeared on June 27 rose from infections that occured on or before June 16, twelve days or more earlier. During this interval the mean temperature was 62.9° F., the mean maximum temperature was 74.8°, the mean minimum temperature 51.1°, the range being from 92° to 40° F. These temperatures coincide moderately well with those given for the greenhouse experiment mentioned above in connection with the incubation period of stem rust in 1929, although the range is 6° F. wider. As there was less cloudiness during the period involved in 1936 than in 1929, a shorter incubation period for the rust would be expected, but probably not much shorter than that which was actually required. Were it not for the comparatively high temperatures that prevailed during the last three or four days of the period, the incubation period would probably have been somewhat longer.

In 1937, a trace of spores—mostly 1 per day, 11 in all—was detected by the slides exposed from June 10 to 18. Light rain fell on June 13, 16, and 18, and the possibility that dew occurred on all but one night seems to have been good. Unless the spores present were non-viable, it would be expected that some of them would cause infection, as the mean temperature from June 13 to 18 was 68.7° F., the temperature range being 51° to 84° F. It seems likely that infections occurring at this time were responsible for the pustules that began to appear on July 1, about two weeks later. As shown in Table 26, some spores were present on June 19 and a light spore shower occurred from June 21 to 24. Rain fell on June 19, 22, and 23, and dew was probably present at night from June 20 to 23. The likelihood is that a moderate amount of infection occurred at this time. From then until a light general infection began to appear, a period of about two weeks, relatively few spores were present in the air, the sky was moderately clear, rain fell only once, and dew seems to have been absent or light on five nights. It would, therefore, seem that the increase of stem rust after July 6 can be traced fairly directly to infections that occurred prior to June 23. From June 19 to July 6, the mean temperature was 69.5° F., with a mean daily maximum of 83.2° and a mean daily minimum of 55.9°F. the range being from 92° to 46° F. In a greenhouse experiment[10], in which inoculations of seedling wheat plants were made on April 29, full pustule development was attained on May 15, after an interval of 16 days. During this interval, the mean temperature was 69.3° F., the mean daily maximum 74.7°, the mean daily minimum 55.3°, the range being from 86° to 52° F., but, as mentioned before, the weather was rather cloudy. In comparison with the temperature conditions in the greenhouse, the extremes in the field for the period discussed are considerably greater and probably tended to delay rust development as much as the slightly higher mean daily maximum tended to hasten it. Apparently, therefore, in 1937, stem rust pustules appeared in the field as early as weather conditions would permit.

[10] See footnote number 9 on page 370.

TABLE 26.—DATA RELATIVE TO THE OCCURRENCE OF STEM-RUST UREDIOSPORES AND WEATHER CONDITIONS EACH DAY AT WINNIPEG DURING A PERIOD OF 18 DAYS IMMEDIATELY PRECEDING THE APPEARANCE OF A LIGHT GENERAL INFECTION IN EASTERN MANITOBA IN 1929, 1936, 1934, AND 1938. NUMBER OF SPORES INTERCEPTED PER 1 SQUARE INCH GLASS-SLIDE SURFACE, PER CENT CLOUDINESS, RAINFALL IN INCHES, MAXIMUM AND MINIMUM TEMPERATURE (FAHR.), TEMPERATURE, RELATIVE HUMIDITY, AND WIND VELOCITY AT 7.00 P.M., AND THE DAYS (INDICATED BY +) ON WHICH THE RELATIVE HUMIDITY AT 7.00 P.M. AND THE DIFFERENCE BETWEEN THE TEMPERATURE AT 7.00 P.M. AND THE MINIMUM TEMPERATURE WERE SUCH AS TO INDICATE THAT THE AIR HUMIDITY REACHED THE DEW POINT DURING THE NIGHT

Factors	June 1929															July 1929		
	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	1	2	3
Number of spores	133	193	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Cloudiness (per cent)	16	66	53	66	60	33	56	66	80	63	53	80	53	20	40	60	46	30
Rainfall (inches)	—	0.32	—	0.04	0.04	0.19	T	—	T	0.06	—	0.28	—	0.10	0.24	T	—	T
Temperature, maximum	94	87	81	72	76	76	65	62	68	67	72	69	74	78	78	70	76	80
Temperature, 7.00 p.m.	90	83	77	60	66	66	64	59	63	62	68	64	69	75	72	65	74	76
Temperature, minimum	62	74	57	54	53	50	46	48	48	50	41	56	50	57	54	50	47	52
Relative humidity, 7.00 p.m.	51	70	36	87	55	60	46	59	63	62	52	75	49	43	60	48	43	48
Wind velocity, 7.00 p.m.	16	25	16	8	10	13	12	9	10	12	5	12	8	14	12	10	5	20
Air dew point reached	+	—	—	+	+	+	+	—	+	—	+	+	—	—	+	—	+	+

Factors	June 1936																	
	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Number of spores	0	0	2	10	0	0	1	0	0	0	0	0	0	0	0	4	0	
Cloudiness (per cent)	85	10	80	55	T	100	100	30	53	0	26	16	30	0	33	16	26	T
Rainfall (inches)	T	0.05	T	T	—	0.29	0.49	—	—	—	—	—	—	—	—	—	0.14	—
Temperature, maximum	74	78	88	83	60	71	54	69	76	73	73	70	78	85	92	80	82	76
Temperature, 7.00 p.m.	65	77	84	73	58	65	53	66	73	63	66	70	73	83	84	75	81	71
Temperature, minimum	43	44	61	65	43	45	52	50	49	48	40	40	40	49	60	67	58	60
Relative humidity, 7.00 p.m.	50	46	45	38	58	51	97	49	50	48	59	36	52	39	50	61	49	42
Wind velocity, 7.00 p.m.	7	14	18	29	6	12	8	7	14	19	9	2	6	8	6	13	6	11
Air dew point reached	+	+	—	—	+	+	+	—	+	—	+	+	+	+	+	—	+	—

TABLE 26.—DATA RELATIVE TO THE OCCURRENCE OF STEM-RUST UREDIOSPORES AND WEATHER CONDITIONS EACH DAY AT WINNIPEG DURING A PERIOD OF 18 DAYS IMMEDIATELY PRECEDING THE APPEARANCE OF A LIGHT GENERAL INFECTION IN EASTERN MANITOBA IN 1929, 1936, 1937, AND 1938. NUMBER OF SPORES INTERCEPTED PER 1 SQUARE INCH GLASS-SLIDE SURFACE, PER CENT CLOUDINESS, RAINFALL IN INCHES, MAXIMUM AND MINIMUM TEMPERATURE (FAHR.), TEMPERATURE, RELATIVE HUMIDITY, AND WIND VELOCITY AT 7.00 P.M., AND THE DAYS (INDICATED BY +) ON WHICH THE RELATIVE HUMIDITY AT 7.00 P.M. AND THE DIFFERENCE BETWEEN THE TEMPERATURE AT 7.00 P.M. AND THE MINIMUM TEMPERATURE WERE SUCH AS TO INDICATE THAT THE AIR HUMIDITY REACHED THE DEW POINT DURING THE NIGHT—*Concluded*

Factors	June 1937												July 1937					
	19	20	21	22	23	24	25	26	27	28	29	30	1	2	3	4	5	6
Number of spores	2	0	3	5	4	9	0	2	0	1	0	0	0	0	0	0	10	180
Cloudiness (per cent)	43	36	T	77	37	33	17	10	43	27	40	20	47	47	57	0	27	30
Rainfall (inches)	0.36	—	—	0.15	0.16	—	—	—	—	—	—	—	—	—	0.24	—	—	—
Temperature, maximum	79	84	76	87	90	80	80	78	83	69	76	82	88	80	85	84	92	87
Temperature, 7.00 p.m.	76	76	76	71	88	75	76	76	72	67	73	80	86	76	79	82	90	79
Temperature, minimum	60	51	53	55	65	62	55	49	57	47	47	46	54	64	58	52	59	73
Relative humidity, 7.00 p.m.	54	45	46	84	66	37	41	34	54	44	45	31	48	72	66	42	38	47
Wind velocity, 7.00 p.m.	16	8	9	9	8	21	20	13	11	10	7	5	12	11	19	5	22	10
Air dew point reached	−	+	+	+	+	−	−	−	−	−	+	+	+	+	+	+	+	−
	June 1938																	
	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Number of spores*	1	—	0	—	5	—	0	—	0	—	18	—	10	—	0	—	1	—
Cloudiness (per cent)	70	46	T	86	100	100	70	T	0	30	56	16	50	77	80	20	37	80
Rainfall (inches)	0.19	0.04	—	0.34	0.04	0.06	—	—	—	0.06	T	0.01	—	—	—	—	—	—
Temperature, maximum	61	69	78	81	63	56	69	78	85	87	91	93	82	82	70	72	74	78
Temperature, 7.00 p.m.	61	65	77	70	52	56	69	76	83	73	82	87	77	73	70	67	72	76
Temperature, minimum	52	37	38	56	52	45	52	46	52	65	66	64	52	59	62	52	38	55
Relative humidity, 7.00 p.m.	60	48	34	76	84	74	58	43	52	90	72	45	37	41	38	46	37	42
Wind velocity, 7.00 p.m.	6	7	9	16	17	10	3	12	13	10	8	14	8	9	14	13	4	7
Air dew point reached	−	+	+	+	−	+	+	+	+	+	+	+	+	−	−	−	+	−

* In 1938, each slide was exposed for a 2-day period.

In 1938, stem rust first appeared on June 22 and a light general infection began to appear on June 27. It is not probable that the spores present from June 19 to 22 were responsible for these infections as the intervening period was too short to permit full stem-rust development, although they undoubtedly were responsible for later appearing infections. The light general infection is probably traceable to spores present on June 13 and 14, although the earliest pustules, appearing on June 22, perhaps arose from spores present on June 9 and 10. Rain fell on June 13, 14, and 15, and as these three days were cloudy and dew was probably present at night on June 13 and 15, infection probably occurred during this time. On this supposition, an interval of 13 to 15 days was required for rust development. From June 13 to 27, the mean daily temperature was 65.7°, the mean daily maximum temperature 77.1°, the mean daily minimum 54.3°, the range being 93° to 38° F. In a greenhouse experiment[11], inoculations made on April 24 gave rise to fully developed pustules 17 days later. The average temperature for the period was 65.5° F., the mean daily maximum temperature 73.8, the mean daily minimum 54.1°, the range being from 87° to 46° F. Daylight hours were less per day and there was perhaps more cloudiness during this period than during that from June 13 to 27, 1938, so that it is not unreasonable to suppose that, under the weather conditions that prevailed during the latter period, rust development in the field would have required from 13 to 15 days.

In view of the comparisons given above, it is probable that, under the conditions that prevailed in the field during June and early July, stem-rust development proceeded as rapidly as could be expected. As far, therefore, as the evidence for these four or five years is concerned, there seems to be little ground to support the supposition that the stage of crop maturity had any significant influence on the time that the rust appeared in the crop.

AMOUNT OF INOCULUM AND TIME OF ARRIVAL IN RELATION TO SEVERITY OF STEM-RUST OUTBREAKS

A stem-rust epidemic arises as the result of many infections on all or the majority of the plants of one or more cereal crops. As each infection is caused by a separate spore, a great many spores are involved in producing the infections. Besides, a great many spores fall to the ground or lodge on non-susceptible plants, so that a much greater number is produced than ever succeeds in infecting cereal crops. An abundance of inoculum is, therefore, a prerequisite of a stem-rust epidemic. Freeman and Johnson (67) point out that if spores are unusually abundant in early summer, the first infections may be heavy and widespread and the chances for an epidemic may be thereby increased. Stakman (189, 193, 195) emphasizes this point in connection with the early spread of spores from infected barberry. Peltier (156, 157) claims that an abundance of initial inoculum is one of the principal factors involved in the development of epidemics in Nebraska. Levine (118) states that only abundant inoculum early in the season is conducive to heavy rust attacks. Stakman (195), in his analysis of the conditions that must exist to permit stem rust to spread from the southern to the northern part of the Mississippi Valley, implies the production of immense numbers of spores in the southern part of that area.

[11] See footnote number 9 on page 370.

As under favourable conditions of temperature, an infection requires approximately a week to produce spores, it is evident that if the initial inoculum is limited the time required for stem rust to reach epidemic proportions in any given area will be considerably longer, other things being equal, than if the initial inoculum is abundant. If to the initial inoculum there is added from time to time increments of wind-borne spores, the time necessary for the development of epidemic conditions will be shortened, and the greater and more frequent the increments, the shorter will be the time needed to attain such conditions.

Relation in Western Canada in Different Classes of Years

In the different parts of Western Canada, for example, in Manitoba or eastern Saskatchewan, the period during which stem-rust inoculum is produced locally is relatively short, and on this account the multiplication of inoculum must be somewhat restricted. The average date for harvesting of wheat to become general in Manitoba is August 7 and in eastern Saskatchewan, August 16. Light general primary infection rarely is present in Manitoba until the first or second week in July, and in eastern Saskatchewan, usually from a few days to a week or more later than in Manitoba. As a rule there is then in these two areas—the most seriously affected ones—only a period of approximately a month in which the stem-rust organism has opportunity widely and intensively to multiply. The organism requires about one week to produce a new generation of spores, consequently, in these two areas, four generations of spores are about all that can be produced in most seasons before the bulk of the wheat crop is too far advanced for much infection to take place. It would appear, therefore, that as a rule stem rust could scarcely reach epidemic proportions unless the initial inoculum arrived moderately early and in considerable abundance, and increments of additional inoculum arrived subsequently from time to time.

Light Rust Years

This conclusion, at any rate, would seem to be supported by the spore-trapping data given in Table 2. It is evident from this table that in the light rust years (1926, 1928, 1931, 1932, 1933, and 1934), the amount of wind-borne inoculum in the last half of June and the first two weeks of July was relatively small. The same is true of 1936, although for economy of space the data are omitted. Because of the pronounced spore shower at the middle of June, the year 1929 is a partial exception to the general rule. However, following that shower and up to July 10, the spore content of the air was low, and continued low except in the northern part of the Red River Valley (represented by Winnipeg), where a moderately heavy infection developed on wheat. Without doubt, lack of inoculum in 1928 was the only factor that prevented an epidemic from developing in that year, as weather and crop conditions appeared to be ideal throughout the

season for stem-rust development. In 1931, weather conditions during the last week of June and the first two weeks of July were very favourable for stem-rust development in Manitoba, particularly in the Red River Valley, although cereal crops were not so dense and tall as in 1928, and after July 20 hot weather hastened the ripening of cereals, but if an abundance of initial inoculum had been present there is no doubt that very serious damage from the disease would have resulted. In the other light rust years, weather or crop conditions were probably less favourable to the development of the disease than in the two years just referred to, but even in these years the likelihood is that, at least in areas where drought was not severe, the lightness of the infection was due more to a lack of early inoculum than to the unfavourableness of weather and crop conditions.

Medium Rust Years

Only data for two medium rust years (1930 and 1937) are given in Table 2. As far as stem-rust development in these years is concerned, the chief characteristic was that epidemic conditions were somewhat late in becoming established, and consequently the earlier sown crops escaped with slight to moderate damage. It will be observed in this table that spores in the atmosphere were relatively few in both years during the latter half of June, and in 1930 continued to be few up to July 10, although only to July 4 in 1937. A similar circumstance obtained in 1925, a medium rust year, in which heavy spore showers occurred around the middle of July and later. In these years, weather and crop conditions (in 1937, only in Manitoba) were favourable to the development of stem rust. Moderately heavy infection (30 to 50% on most plants) in the field appeared in 1925 during the last few days of July and early August, in 1930 during the fourth week of July, and in 1937 during the third week of July. The delayed appearance of moderate infection in the field seems, therefore, to be definitely related to the late arrival of inoculum in considerable abundance. When a moderately heavy infection becomes established, sufficient spores are perhaps produced locally to ensure the development of maximum infection on those crops that require two or three weeks more to mature, but increments of inoculum from outside make that result more certain of being attained.

Heavy Rust Years

In contrast to the comparatively late arrival of inoculum in considerable quantity in the medium rust years, it is evident from Table 2 that at least in two of the epidemic years (1935 and 1938) inoculum was plentiful in the last week of June in one, and during the last half of June in the other; especially in the Red River Valley (represented by Morden and Winnipeg). A light general infection developed in Manitoba in 1935 by July 10 (in the southern part of the province by July 6) and in 1938 by July 5. Actually, in 1935, infection was becoming heavy by July 16, so that from July 2 and 3 when infection first appeared, there was a continuous and rapid increase

in the amount of infection. In 1938, moderately heavy infection was not established until about July 16 and heavy infection by July 25. It would appear that in the latter year the great increase of inoculum from July 9 onward was responsible for the rapid increase of infection after the middle of July. In the third heavy rust year (1927), inoculum during the last half of June and the first half of July was not particularly plentiful. Stem-rust development was slow. A light general infection was present by July 18, after which there was little change until about the last of July, when the number of infections showed considerable increase. Inoculum became abundant in late July, but owing to comparatively cool weather heavy infection did not develop until after the middle of August. This extended period of rust development was made possible by the exceptionally slow rate at which the crop matured in that year. Had the crop ripened about the average time, no epidemic would have developed.

There is a rather close relation in all these years, except 1929, between the time the inoculum—much of which must have been introduced—became plentiful and the time of rapid increase in the amount of infection. A sudden increase in the amount of infection occurred in most years with marked regularity about a week after inoculum was abundant, a fact which indicates that in most years weather conditions were at least tolerably favourable for infection during a shorter or longer period following the arrival of inoculum. There can be no doubt that the amount of wind-borne inoculum and the time of its arrival are very intimately related to the severity of the infection present on the crop at maturity.

Years 1919 and 1920

The years 1919 and 1920 are probably not exceptions to this general rule. In both years, stem rust was epidemic in the Upper Mississippi Valley (113, 207), and consequently it would be expected that inoculum in considerable abundance would have been blown northward in those years. In Western Canada, however, the records available indicate that the outbreak in 1919 was considerably less severe than in 1916 (one of the worst rust years), and in 1920 somewhat less than in 1919. On this account, 1919 has been classed as a medium rust year and 1920 as a light rust year. As mentioned earlier in this connection, it might have been just as nearly accurate to have classed the former as a heavy rust year and the latter as a medium rust year.

In Manitoba and eastern Saskatchewan, crop conditions in the spring of 1919 were good, but the weather became exceptionally warm in June, being at different stations from 4° to 7° F. above average in Manitoba and from 6° to 10° F. above in eastern Saskatchewan. During July, the temperature continued high, being from 2° to 6° F. above average in both areas, and rainfall was below normal except in eastern Manitoba, where infection became very severe. In western Manitoba and eastern Saskatchewan, heat was reported to have done about as much damage as the rust.

In 1920, the June rainfall was less than average in eastern Manitoba, about average in Western Manitoba, and considerably below average in eastern Saskatchewan, while the temperature was slightly above average in eastern Manitoba but about average in the other two areas. Throughout Manitoba, temperatures in July were from 1° to 4° F. above average and the rainfall, except at two or three points, was very considerably below average; while in eastern Saskatchewan the temperature ranged from 1° to 7° F. above average, with rainfall at some points somewhat above, but at most points below average. Generally speaking, the season was characterized by heat and drought. Nevertheless, stem rust was prevalent, being more abundant than could well have been expected under the conditions.

It is evident that in these two seasons weather conditions were not favourable for rust development, excepting in 1919 in eastern Manitoba where, as a matter of fact, stem rust was severe. Judged by the weather conditions that prevailed, infection should have been extremely light (apart from the exception just mentioned). In spite of these conditions, stem-rust infection in 1919 approached, if it did not reach, epidemic proportions, and in 1920 it was surprisingly heavy for the conditions that prevailed. In both seasons the crop ripened unduly early. It would seem that only in the presence of abundant wind-borne inoculum was it possible for such an amount of infection to develop as did develop in these two years.

Cool Seasons

Heavy stem-rust infection can develop under moderately cool conditions, and some evidence of this fact has been obtained in the present investigation. It would probably be more correct to say that the disease develops in spite of the cool weather. Such weather not only retards rust development but also the development of the host plants, so that the plants remain longer green and thus the organism is given a longer period in which to develop and spread. Apparently one of the conditions necessary for the occurrence of heavy infection under cool conditions is the presence of an abundance of wind-borne inoculum to cause mass infection. Under cool conditions, rust development probably proceeds too slowly to permit locally produced inoculum to be a factor of much consequence, although such inoculum may, in turn, become wind-borne inoculum and of consequence for some other area. For example, in spite of the cool weather in 1904, rather severe infection developed in Manitoba and eastern Saskatchewan, undoubtedly as a result of a destructive and widespread outbreak in the Upper Mississippi Valley, and this condition in the latter area was undoubtedly largely brought about by wind-borne inoculum from farther south where temperatures were more favourable for stem-rust development.

INTERRELATION OF SOME FACTORS AFFECTING STEM-RUST DEVELOPMENT IN WESTERN CANADA

In the foregoing sections of this paper, an attempt has been made to discuss separately various factors in their relation to the development of

stem rust in Western Canada. It has been shown that primary infection is almost exclusively initiated, if in recent years not entirely, by wind-borne inoculum, and that during June and the first three weeks of July such inoculum is almost invariably most abundant during periods of south wind. Considerable agreement is found year by year in the intensity of infection in the Upper Mississippi Valley and Western Canada, and also in the relative prevalence of the more commonly occurring physiologic races in these two areas. Most years of heavy stem-rust infection are associated with years in which spring and summer rainfall, as well as July temperatures, are somewhat above the average. From late June to early August, minimum temperatures tend to be higher in the heavy rust years than in the light rust years. In most of the light rust years, the rainfall for the spring and summer is slightly below average. Infection is almost invariably more abundant in Manitoba and eastern Saskatchewan than in western Saskatchewan and Alberta.

Such relationships are not fortuitous, but are the expression of a closely interrelated sequence of events. The prevalence of spores during periods of south wind arises from the fact that cereal crops mature earlier, and stem rust develops earlier, in the Upper Mississippi Valley than in Western Canada. South winds sweeping over rusted grain in the former area carry spores northward into the latter area. Consequently, the physiologic races prevalent in the one would be expected to be the prevalent races in the other. A severe outbreak of stem rust in the Upper Mississippi Valley provides an abundance of inoculum for distribution northward in Western Canada, and hence increases the chances of a severe outbreak in that area. Moreover, both areas have largely the same source of moisture—warm moist air from the Gulf of Mexico and the Caribbean Sea, brought northward by south winds. There is, therefore, a tendency year by year for moisture conditions in the two areas to be similar. For the growing season, temperatures, too, are not markedly different, although in the Upper Mississippi Valley, the season is somewhat earlier than in Western Canada. The expectation, therefore, would be to find a good deal of agreement year by year in the intensity of infection in the two regions.

There is a close interrelation between weather conditions and crop conditions, and between these and the amount of stem rust that develops. The tendency for stem rust to be more prevalent in growing seasons with high rainfall arises as a result of the interaction of a number of factors. A plentiful supply of moisture induces rapid succulent crop growth, resulting in tall, dense stands of grain. Deficient rainfall has the opposite effect. Air circulates less freely within a tall, dense stand of grain than within a thin, short one, so that following a rain or heavy dew the plants and the air surrounding them dry much less rapidly in the former than in the latter type of crop. Conditions favourable for infection are, therefore, present for a longer space of time, and the more frequently rain occurs the more often are such conditions present. Furthermore, stem rust develops more vigorously and produces larger pustules in succulent (7, p. 239) than in

drier firmer tissue, so that the pustules produce more spores, and, therefore, more inoculum is available for distribution in wet than in dry seasons. Vigorous crop growth is dependent on suitable temperature conditions. So also is rapid rust development. A tendency, therefore, would be expected in the heavy rust years for the temperature during the critical month for the disease in Western Canada to be somewhat higher, that is to say, somewhat closer to the optimum temperature, than in the other two classes of years. Given suitable conditions of moisture and temperature, the amount of infection is dependent on the amount of inoculum and the time of its arrival in relation to the maturity of the crop. The failure of stem rust, therefore, to attain equal severity in Alberta and western Saskatchewan with that in eastern Saskatchewan and Manitoba seems to be attributable to the lighter rainfall and lower temperature in the former areas during the growing season, and particularly to the lesser amount and later arrival of inoculum.

Some of these relationships can be inferred from a study of Table 27, which gives for each day from June 23 to July 15 the hours of south wind (SE., S., SW.), the number of stem-rust spores intercepted by one square inch surface of glass slide, the rainfall, and the daily maximum and minimum temperatures, at Winnipeg, for two light rust years (1928 and 1931), two medium rust years (1930 and 1937), and two heavy rust years (1935 and 1938). This table shows that there is a distinct tendency for high concentrations of spores to be present in the atmosphere during periods of south wind. As such winds usually carry considerable moisture, there is, as might be expected, a tendency also for rainfall to be rather frequently associated with them. For example, in 1935 a south wind blew all day on June 23 and 24 and during the greater part of June 25. A heavy spore shower occurred on June 24 and continued into June 25. Over one-half inch of rain fell on June 24, a trace fell on June 25, and a light shower on the following day. A similar relation is evident in the same year between June 28 and July 2, and in 1938 between June 27 and July 1, as well as for shorter periods in other years. Thus two of the most important factors conducive to heavy infection, inoculum and moisture, are frequently brought together in proper sequence. Absence or paucity of spores during periods of south wind is mainly attributable either to the lack of inoculum farther south, as was the case on June 30 and July 1 and 2, 1928, or to rain washing the air comparatively free of spores, as evidently happened on July 3 to 6, 1938.

Furthermore, there is a tendency for temperatures to rise with the occurrence of south winds. This happens as a result of the arrival of warm air from the south. An examination of Table 27 shows that this happens rather regularly when south winds prevail for two or three days, as they frequently do. Thus, night temperatures tend to approach more nearly the optimum for infection. Besides, the higher temperatures tend to stimulate the rapid development of those infections that have already taken place. On the other hand, even though weather conditions are

favourable for stem-rust development, the disease can make little headway unless inoculum is abundant. This fact is emphasized by the comparative lightness of the attack in 1928 and 1931. Although weather conditions were favourable for stem-rust development throughout the growing season in 1928 and in late June and early July in 1931, heavy infection did not develop, largely it would seem, through lack of inoculum.

The occurrence of south winds with their concomitant weather conditions—higher moisture content and temperature—may give rise to short periods of warm humid, "muggy," weather, frequently referred to by farmers as "rust weather." Such weather conditions are generally found associated with the south-eastern sector of an atmospheric low pressure area as it passes eastwardly across the continent. This is the sector into which the warm air from the south, the "tropical" air of the meteorologists, flows. If stem-rust inoculum is present in the regions over which the south winds blow, it is carried northward by them. When the tropical air meets the cooler, and hence heavier, "polar" air, it is forced to rise, as as up an inclined plane, and becoming cooled deposits its moisture as rain. Rain occurs also on its western flank, where the cooler polar air pushes under it and forces it aloft (Figure 13). There is a good chance, therefore, that the introduction of inoculum and the occurrence of rain will be associated with periods of warm humid, "muggy," weather. The belief that this sort of weather is a precursor of stem-rust outbreaks is, therefore, in the main, fully justified, although the weather is not the direct cause of the outbreaks.

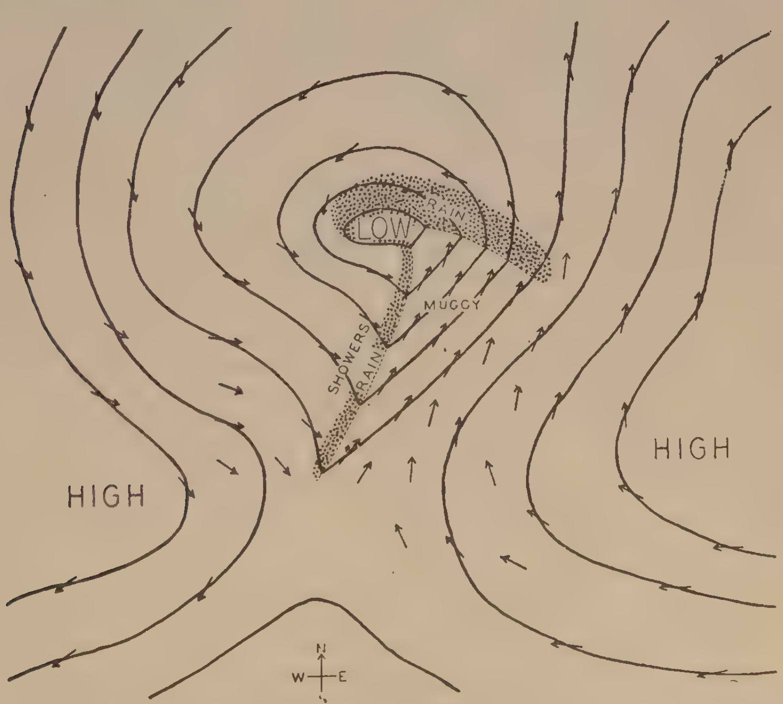

FIGURE 13. Diagrammatic representation of a low pressure area flanked by two high pressure areas. The wind direction in the different parts is indicated, as is also the humidity conditions often associated with the occurrence of south wind.

TABLE 27.—INTERRELATION OF SOME FACTORS INFLUENCING STEM-RUST OUTBREAKS IN WESTERN CANADA. HOURS OF SOUTH WIND, NUMBER OF UREDIOSPORES INTERCEPTED, RAINFALL, AND AVERAGE TEMPERATURE (FAHRENHEIT), EACH DAY AT WINNIPEG, MANITOBA, FROM JUNE 23 TO JULY 15, FOR TWO LIGHT, TWO MEDIUM, AND TWO-HEAVY-RUST YEARS

Year	Factors	June								July														
		23	24	25	26	27	28	29	30	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1928 (Light)	South wind	0	0	0	2	15	15	2	24	24	15	1	5	19	1	0	0	4	4	5	0	11	24	18
	Spores	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	2	—	2	43	—
	Rainfall	—	—	—	—	—	T	—	T	—	0.39	—	T	0.21	1.61	—	0.90	0.03	—	0.02	—	—	—	—
	Temperature	62	60	60	64	65	68	71	71	73	71	66	66	69	71	67	62	62	66	69	68	69	72	76
1930 (Medium)	South wind	2	12	10	0	3	11	13	1	19	24	23	8	0	8	22	4	14	0	10	0	0	24	18
	Spores	—	2	—	—	—	—	—	—	5	4	5	2	—	—	8	—	5	—	3	5	17	161	480
	Rainfall	—	0.06	—	—	T	0.05	T	—	0.86	1.29	T	—	—	—	0.06	T	—	—	T	—	—	—	—
	Temperature	65	64	64	64	66	64	57	65	64	67	69	71	69	71	74	80	80	72	74	71	64	66	77
1931 (Light)	South wind	23	13	19	13	19	23	9	4	7	8	0	8	11	12	0	2	9	24	24	13	14	0	4
	Spores	—	—	—	—	1	1	2	—	—	—	—	—	—	—	2	1	—	21	—	—	1	1	8
	Rainfall	—	0.16	—	—	0.22	T	—	0.03	0.07	—	—	1.07	0.01	0.02	0.05	T	0.03	—	0.65	0.01	0.03	—	0.26
	Temperature	64	69	73	71	78	86	83	82	77	68	60	60	65	63	59	60	64	69	71	68	71	70	73
1935 (Heavy)	South wind	24	24	20	5	0	23	24	23	24	17	5	18	0	2	19	17	15	10	3	0	1	9	14
	Spores	9	240	52	—	—	10	17	37	7	22	7	12	5	—	1	—	3	—	3	12	7	6	50
	Rainfall	—	0.56	T	0.18	—	—	T	0.05	—	0.16	—	0.52	T	—	—	0.16	—	0.76	0.01	—	0.08	—	—
	Temperature	62	68	66	62	60	65	73	76	77	74	78	69	66	64	65	68	71	75	70	69	69	68	72
1937 (Medium)	South wind	22	6	12	6	11	0	8	16	21	0	11	6	24	10	4	19	6	0	0	0	0	3	0
	Spores	4	9	—	2	—	1	—	—	—	—	—	1	10	180	2	1	—	82	—	—	1	12	1
	Rainfall	0.16	—	—	—	—	—	—	—	—	—	0.24	—	—	—	—	0.10	1.32	—	—	—	—	0.06	0.48
	Temperature	80	63	61	61	69	65	72	68	71	72	72	68	76	80	71	71	68	71	72	73	72	69	68
1938 (Heavy)	South wind	0	0	0	3	15	24	14	14	22	0	18	17	20	15	2	0	17	5	23	16	0	7	3
	Spores	—	—	—	1	—	86	—	328	—	2	—	—	—	4	—	3	—	140	—	247	—	113	—
	Rainfall	—	—	—	—	—	0.17	0.02	—	0.07	0.07	0.06	0.65	0.70	0.08	0.09	—	0.02	—	—	0.06	0.02	0.03	—
	Temperature	71	66	62	56	67	66	67	72	70	71	75	75	73	72	72	63	63	68	71	78	63	67	71

DISCUSSION

The main purpose of the investigation was to determine the source of stem-rust infection in Western Canada and to ascertain the cause of the variation from year to year in the intensity of the infection. The results of the investigation are summarized at the end of this paper. It is only necessary here to mention a few points that were not earlier given consideration.

There is abundant evidence to indicate that in Western Canada early infections arise largely or entirely from wind-borne urediospores, and that in some years and probably in all these spores originate at a considerable distance from this area—four or five hundred miles and in some years even farther. That they can be carried for long distances is not surprising. They are extremely small, and can readily be carried about by winds. Gassner (72) suggests that the minute echinulation of the surface of the spores increases their buoyancy, and thus they do not settle to earth so readily as if the surface were smooth. Ukkelburg (220) measured their rate of fall in still air, and found it to be 11.5 millimeters per second, approximately 136 feet per hour. He calculated that urediospores at a height of 5,000 feet and carried by a wind of 30 miles per hour would have a theoretical dispersal distance of between 1,100 and 1,200 miles. If the spores were at a higher level, or if the wind velocity were greater, the distance would be increased.

Urediospores of stem rust in large numbers reach a height of one mile (5,280 ft.) above the earth's surface and sometimes even nearly double that height. This was shown by Stakman and co-workers (203) in an investigation of the spore content of the upper air over the Mississippi Valley and by Peturson (162) in connection with the present investigation (Table 5) in Western Canada. Wherever stem rust is abundant, tremendous numbers of urediospores are produced, and, if not wet with dew or rain, they are readily blown away by winds, even by gentle breezes, but particularly by strong sudden gusts, which are of frequent occurrence on hot dry days. On such days, too, small whirlwinds are common, and strong upward convection currents are numerous. These currents rise at a much faster rate than the force of gravity causes the spores to fall, and hence the spores are carried aloft, probably to about as high levels as the rising air attains. Somewhere about the two-mile level, there is usually a marked thinning out in the number of fungal spores present in the air (136, 162, 198, 203, 233), but some types of spores have been found at a height of about four miles (166, 167).

Of course, it is a general rule that what goes up must come down, and rust spores are no exception. Always there is acting on them the force of gravity, but owing to their buoyancy their rate of fall in the lower air levels is very slow. According to Ukkelburg's (220) data, urediospores in still air would require more than a day and a half to settle to the ground from a height of one mile. While descending, as a result of the effect of gravity, they may, however, meet ascending air currents, and thus their sojourn in the atmosphere may be considerably prolonged. They may be brought down, however, from high levels relatively quickly by descending convection air currents. The descending cooler air, being of greater

density than the warm air at the earth's surface, displaces it, thus giving rise to the ascending currents. As the warm air rises, it gradually becomes cooler and, if it contains considerable water vapour, this vapour condenses. Condensation apparently can only occur if there are present particles of solid matter, such as of dust or smoke, to serve as "nuclei" on which the moisture can condense. Rust spores carried aloft can, no doubt, serve as such nuclei, and, as condensation of moisture on them proceeds, their buoyancy decreases and they tend to fall more rapidly than would dry spores. If the amount of condensation is pronounced, droplets of water may thus be formed and the spores may be brought down quickly in the resulting rain.

No attempt seems yet to have been made to investigate the dispersal pattern of spores liberated into the air at any particular place and height, and hence any discussion of the matter must be largely theoretical, although certain deductions can be drawn from observation of the infection pattern of stem rust in the field. Where a localized center of infection occurs, new infections, as a rule, are most numerous in the vicinity of the center, and become fewer in number as the distance from the center increases, the greatest distance of spread being in the direction that the prevailing wind blows (108, 113, 141, 158). Where an extensive area of heavy infection exists, the same general pattern of spread seems to obtain, but on a proportionately larger scale. From such an area, enormous numbers of spores are carried aloft, some to greater, some to lesser heights. As already indicated, the spore concentration is much greater at the lower than at the higher levels. If, therefore, the wind were blowing at the same rate at all levels, the spores in the lower levels would settle first, those at the higher levels later and at a greater distance from their place of origin. Owing, however, to the retarding effect of friction, and particularly to the obstruction offered by mountains, hills, forests, and large cities, the wind velocity is much reduced near the ground. The retarding effect decreases with increased height, so that at a height of 2,000 feet the velocity is considerably greater than at the surface of the earth. The tendency, therefore, is for the spores at the higher levels, in contrast with those at the lower levels, to be carried farther in proportion to their height, and, as they are less numerous, to be spread more thinly over the area where they finally settle. No doubt, many of the spores that settle early are picked up again by the wind and rising air currents and are carried farther onward, proceeding as it were by a succession of hops, and in diminishing numbers, but their rate of progress would be a good deal slower than that of those carried at the higher levels.

This theoretical pattern of spore spread seems to correspond, as would be expected, with the ascertained data, although such data are very limited. Lambert (113) reports that slides exposed at three feet from the ground for 20 hours at distances of 3, 6, and 69 feet from a heavily rusted planting of barberries, caught 160,000, 33,000, and 210 aeciospores, respectively, while a few days later slides exposed for a week at a distance of 3,300 feet intercepted 3,000 spores (approximately 355 per each 20 hours), and a slide 1 mile away collected a few spores after a 2-day exposure. Stakman (193) states that, in southern Minnesota, slides exposed for different periods of

time at 4 feet above ground level and at different distances from a heavily rusted barberry bush, intercepted aeciospores per square foot as follows:

In 2 days, at distance of 3 feet	7,000,000 spores
In 3 days, at distance of 90 feet	45,000 spores
In 1 week, at distance of 5/8 mile	144,000 spores
In 1 week, at distance of 1 mile	100,000 spores

The number of aeciospores intercepted would be expected to vary considerably from day to day, depending on moisture conditions, and wind direction, and on the occurrence of upward air currents. As the distance from the source increased, the number of spores present in the air would undoubtedly tend to diminish.

Owing to the fact that the distribution of stations at which slides were exposed in Western Canada was more largely east and west instead of north and south, the slide-exposure data (Table 3) are of comparatively little value in checking the correctness of the theory in respect to wind-borne spores from the south, the direction in which the source of the early arriving inoculum lies. This deficiency is compensated to a slight extent by certain data for points in the Upper Mississippi Valley. Stakman (193) reports that during a strong south wind on June 10, 1929, 600 urediospores per square foot (between 5 and 6 spores per sq. in.) were caught near the level of grain plants in southern Minnesota, and that on June 16 the number was 800 per square foot. On July 4 and 5, about 3,800 per square foot (26 or 27 spores per sq. in.) were deposited at Fargo, N.D. At none of the stations in Manitoba or Saskatchewan at which slides were exposed in 1929 were any spores detected on June 10 or on July 4 and 5, excepting at Indian Head, Sask., where, on June 10, two spores were intercepted. On June 16 and 17, however, urediospores were present in Manitoba (but not in Saskatchewan) in relatively high concentrations (Table 3). It is evident, therefore, that the spore shower which occurred on June 16 in southern Minnesota continued northward into Manitoba on June 16 and 17, but that the ones on June 10 and July 4 and 5 did not.

Why spores should be present in Manitoba on June 16 and 17 and not on the other dates may be open to more than one explanation, but the most probable one is based on the circulation of the air on the dates in question. On June 16 and 17, a high atmospheric pressure system was present over the eastern and a low pressure one over the western part of the continent (Figure 10), so that a strong south wind blew up the Mississippi Valley for a great distance into Manitoba. On June 10, however, a low atmospheric pressure system was centered over northern Manitoba and Saskatchewan, with the result that a westerly wind was brought to southern Manitoba and a north-westerly one to southern Saskatchewan. Spores, therefore, present in the atmosphere over southern Minnesota would be carried in a north-eastern direction, towards north-western Ontario. A similar explanation holds for July 4 and 5. On the first of these dates, a low pressure area was situated to the north-east of Winnipeg, so that in Saskatchewan and Manitoba the wind blew from the north-west. On the second date the depression had moved farther eastward, as a result of which the weather in southern Saskatchewan and Manitoba was relatively calm, any wind present being chiefly from the west.

Two or three other instances may be given. Stakman (195) relates that strong south winds beginning on June 20, 1935, culminated in a heavy spore shower on June 24 in the State of Minnesota. Reference to Table 3 will show that on the latter date a high concentration of spores was present in the air over Winnipeg. The concentration was much less at Morden, and still less at Brandon, but such differences in spore number are common. In 1937, he (196) states that spore showers occurred in late May in the Upper Mississippi Valley and that there were fairly heavy ones in certain places about June 12. From June 18 to 24 inclusive, spore showers were rather heavy in much of this area, 5,000 spores per square foot (approximately 35 per square inch) being present on June 24 at Brookings, S.D., and on June 23 at Fargo, N.D., and during a 24-hour period (June 23-24) at St. Paul. It will be seen in Table 2 that some spores were present at Morden and Winnipeg on June 12 and also from June 18 to 24. A light, but distinct, spore shower occurred on June 23 at Winnipeg. The number of spores present in Manitoba between June 18 and 24 was considerably less than in the Upper Mississippi Valley, but this circumstance is probably due to the fact that, except on June 18 and on June 22 and 23, the high and low atmospheric pressure areas were not in a suitable position to bring a south wind from far down the Mississippi Valley, and consequently there was probably not a high concentration of spores present in the air, and hence the number that came as far north as Winnipeg was relatively small. At Winnipeg, on June 20, 21, and 24, there was, respectively, only 5, 2, and 6 hours of south wind. According to Stakman and Hamilton (202), heavy spore showers occurred in the Upper Mississippi Valley in 1938 on June 13 and 14. At Fargo, N.D., 1,248 spores per square foot (about 9 per sq. in.) were caught on June 13. From Table 2, it is seen that during the 2-day period June 13 and 14, the number of spores caught at Morden was 29, at Winnipeg 5, and at Brandon 8, per square inch.

There can be no doubt that the spore showers that occurred in Manitoba on these occasions were part and parcel of the showers that occurred in the Upper Mississippi Valley. They occurred during periods of south wind, and as indicated by Stakman, and Stakman and Hamilton, the spores constituting the showers, originated in infected areas lying to the south, apparently considerably far south, of the Upper Mississippi Valley. It is clearly evident, then, that under some circumstances spores originating in one area may be dispersed in considerable numbers a very long distance.

When once viable spores arrive in any district, it might be expected that whenever moisture and temperature conditions are favourable infection of susceptible crops would proceed uninterruptedly so long as such conditions persist. There seems to be the possibility, however, that the opportunities for infection to occur are more restricted than is usually supposed. For example, Weston (234, 235) found that in bright sunlight urediospores floating on water failed to germinate, but they germinated under conditions of low light intensities, and in direct sunlight when they were covered with green and blue filters. Apparently, then, even though moisture, either as dew or rain, is present on plants during the day, little or no infection would occur on those parts of the plants directly exposed to sunlight. Hart (81) and Hart and Forbes (82) found that closed stomata largely excluded the germ tubes of stem-rust spores, so that at night when

moisture conditions are likely to favour infection, the stomata remain closed and little infection can occur. In this connection, it may be mentioned that Allen (3, 4) found that in Kanred wheat only about 10% of the germ tubes succeed in entering the stomata, a fact which she attributed in part to the naturally small stomatal openings of this variety.

Closure of the stomata during the day may possibly also interfere occasionally with infection, but probably not to any very appreciable extent. The stomata of cereal plants are usually open in the morning, gradually close in the afternoon, and remain closed at night. Loftfield (122) found that there is a tendency for cereals to operate with many of their stomata closed, all being open only when the weather is cool, rather humid, and with sunlight of moderate intensity. Under unfavourable conditions, such as low atmospheric humidity or drought, the stomata may remain closed practically all day. This finding is in agreement with that of Maximov and Zernova (125), who showed that under drought conditions the stomata of wheat plants may remain closed the greater part of the day, opening only for an hour or two in the morning. If then, in a dry period, spores were present on the plants, and an opportunity for germination occurred during the day, infection might not be able to take place because of the closed stomata.

Epidemics of stem rust have been found usually to develop in growing seasons with comparatively high temperatures (113, 207, 215, 222, 224, 238), but it would seem that high temperatures must have less effect in some areas than in others on the ultimate amount of infection that may develop. Within limits, an increase in temperature accelerates the rate of stem-rust development. Stakman and Levine showed (208) that rust development is retarded 1 day for every 5 degrees the temperature falls below 66.5° F., and for every 10 degrees it rises above 70° F. At 66.5° F., fresh infections of stem rust require, say, about 1 week to produce spores, whereas at 61.5° F. they would accordingly require 1 day longer. During a period of 7 weeks, therefore, one more generation of spores could be produced at the former than at the latter temperature. On this basis, therefore, it would seem that before high temperatures could be effective in influencing the amount of rust present on the crop, infection would have to be present in an area for a period of approximately 7 to 8 weeks, that is to say, long enough to permit the production of an extra generation of spores. One additional generation, of course, may convert what would otherwise be a moderate infection into one of extreme severity.

Probably, therefore, the influence of warm temperatures on the amount of infection is most evident in areas where the inoculum must be built up from small beginnings, as it must be in areas where the source of infection is isolated spots of overwintered rust or infected barberry, and where the season is sufficiently long to permit the influence of temperature to find expression. For example, stem rust may start spreading from overwintered centres of infection in Texas during the latter part of April (113), and gradually spread northward up to the Mississippi Valley, finishing its course of destruction in that area with the ripening of crops in the northern part of Minnesota and North Dakota in early August, a period of approximately 15 weeks. With favourable moisture conditions, two more generations of spores could be produced during this period at the higher (66.5° F.)

than at the lower (61.5° F.) temperature. In the northern Mississippi Valley States, stem rust frequently begins to spread from infected barberries to cereals and grasses during late April and early May (189, 205). Between then and the time crops ripen in northern Minnesota and North Dakota, there is sufficient time, with a temperature of 66.5° F., for the rust to produce at least one generation of spores more than could be produced if the temperature during the period was 5 degrees lower.

Where the developmental period of stem rust on crops is less than 7 weeks, there would probably be insufficient time for an extra generation of spores to develop, even though temperatures were optimum. For example, in Western Canada, there is, on an average, a period of about 4 or 5 weeks in which stem rust has an opportunity to multiply on the bulk of the crop. This is largely due to the fact that the grain-growing area has its greatest extent east and west, so that much of the crop ripens about the same time. A delay of 2 or 3 weeks in the ripening of the crop, such as happened in 1927, would undoubtedly give opportunity for the production of one or two extra generations of spores, and a consequent steep increase in the amount of infection. In 1927, however, the extra spore generations were made possible by the slow maturing of the crop owing to cool damp weather, not through an acceleration in rust development due to high temperatures. The influence of high temperatures on the intensity of stem-rust infection in Western Canada appears to find expression largely in the increased amount of inoculum that may be induced by high temperature in the Mississippi Valley and thus made available for wind dispersal into Western Canada. If the somewhat higher temperatures in July, of the heavy rust years in the latter area, had any marked effect on the destructiveness of the rust in these years, the effect was probably brought about by a physiological disturbance in the plants themselves as a result of higher loss of water (from plants and soil), rather than by an appreciable increase in the amount of infection induced by high temperatures.

Finally, it may be observed that, according to the meteorological data presented in this paper, years in which stem rust was of moderate to severe intensity in Western Canada were not strikingly different in respect to weather conditions from at least some of the years in which stem rust was of comparatively little consequence. The mean temperature for the 3-month period, June to August, was practically the same for the three classes of years, and although the mean temperature for July in the heavy rust years (69.4° F.) was slightly greater than in the medium (67.9° F.) or the light (67.8° F.) rust years, July temperatures in practically all years were sufficiently high to promote vigorous rust development. Spring and summer rainfall, on an average, was higher in the heavy and medium russ years than in the light rust years, but to a considerable extent the excest in the former two classes of years is attributable to the exceptionally heavy precipitation in one or two years of each class. Likewise, there were, on an average, more days with rain during the three summer months of the heavy and medium rust years than of the light rust years. Whether or not dews were more frequent or copious in one class of year than in another, is not known. Broadly speaking, it would seem that those meteorological factors that are usually regarded as influencing stem-rust development, tended to be, on an average, slightly less favourable in the light rust years

than in the other two classes of years. Nevertheless, it would seem that the actual severity of the disease in most years was more closely related to the amount of wind-borne inoculum that arrived and the time of its arrival than to any special weather conditions that prevailed.

SUMMARY

1. A study has been made of the epidemiology of stem rust, particularly of wheat stem rust, in Western Canada.

2. The disease regularly appears first in southern Manitoba, more often than not in the Red River Valley, and later farther northward and westward, the time of its appearance in Manitoba being late June or early July and in Alberta a month or more later. The area most severely affected is Manitoba and eastern Saskatchewan.

3. Local sources of infection are virtually absent. Barberry, although never an important source of infection in Western Canada, had been eradicated by the time the present investigation was undertaken; and no actual case of overwintering has ever been established, although occasionally a low percentage of urediospores may survive the winter. All spore viability seems to be lost before new growth of grasses or cereals is available for infection in late spring and early summer.

4. Almost invariably inoculum is present in the air earlier over Manitoba, usually first over the Red River Valley, than over Saskatchewan, and over Saskatchewan earlier than over Alberta. In any given district, inoculum has always been found present in the air in advance of infections in the field.

5. Initial inoculum consists largely, if not entirely, of wind-borne spores that originate outside of Western Canada. From time to time subsequent influxes of spores arrive to augment the locally produced inoculum arising as a result of infections by the earlier wind-borne spores.

6. The similarity year by year in the amount of infection and in the physiologic races present in Western Canada and in the Northern Mississippi Valley indicates strongly that the bulk of the wind-borne inoculum originates in the latter area.

7. There is an evident association between years of high spring and summer rainfall and years of medium and heavy stem-rust infection, although the association is not necessarily a close one and seems to be dependent on the presence of some other factor or factors, the chief one apparently being the amount of inoculum. The excess rainfall of the medium and heavy rust years over the light rust years, is not concentrated in any one particular month but is spread over the 5-month period April to August, the April to May and July rainfall, however, being more consistently above average than the June and August rainfall.

8. Similarly, years with an above-average frequency of days with rain during the spring and summer months tend to be associated with years of medium and heavy stem-rust infection. The association does not seem to be close and seems to be dependent on the amount of inoculum that is present.

9. Misty and foggy weather is of comparatively rare occurrence in Western Canada and is, therefore, of little consequence in the promotion of stem-rust epidemics in this area.

10. A tendency seems to be evident for the relative humidity to be slightly higher in years of medium or severe outbreaks than in years when infection was less pronounced, but, probably not high enough to have any appreciable influence on the amount of infection.

11. The frequent occurrence of nights with copious dew in Western Canada is undoubtedly of importance in promoting spore germination and plant infection in this region.

12. For the growing season, the mean temperature in Western Canada tended to be slightly higher in light rust years than in heavy rust years, but slightly lower than in medium rust years. On the other hand, the mean temperature for the month of July in the bad rust area was slightly higher in the heavy rust years than in the light rust years, but probably not sufficiently higher to affect appreciably the amount of stem rust.

13. The mean minimum temperature for the period June 20 to August 4—the period in which stem rust makes most rapid development and spread in Western Canada—tended to be somewhat higher in the heavy rust years and to some extent in the medium rust years than in the light rust years. The chief effect of the lower minimum temperature in the light rust years is probably to retard rust development rather than to decrease the number of infections.

14. No relationship appears to exist in Western Canada between the number of hours of bright sunlight during the growing season and the occurrence of stem-rust epidemics, there being apparently sufficient sunlight in any season to promote vigorous rust development.

15. A close association is evident in Manitoba between the occurrence of periods of south wind and the occurrence of high stem-rust (and leaf-rust) spore concentrations in the air during the period June 12 to July 20. The association is somewhat less evident in Saskatchewan and seems largely to disappear in Alberta.

16. Although the number of hours, as well as of days, with south wind during this period were slightly greater in the heavy rust years than in the light rust years, the excess has probably no particular significance in respect to the number of spores introduced.

17. Broadly speaking, it does not appear that winds favouring the introduction of spores into different parts of Western Canada were more frequent or of greater duration in heavy rust years than in light rust years.

18. Among the factors contributory to the occurrence of more frequent and severe outbreaks of stem rust in Manitoba and eastern Saskatchewan than in western Saskatchewan and Alberta, may be mentioned, in respect to the former areas, their closer proximity to the source region of inoculum, greater number of hours of wind favouring inoculum introduction, and their somewhat higher rainfall and temperature. The first two of these factors tend to ensure a greater abundance of inoculum to those areas.

19. Field infection of wheat in Manitoba, and, as far as known, in the other two provinces of Western Canada, occurs in an occasional year at the time wheat is heading, but in most years after this crop has come into head. Nevertheless, the time at which field infections appear seems to be determined, not by the stage of crop maturity, but by the time of inoculum arrival and the subsequent weather conditions.

20. To a marked extent the establishment of epidemic conditions in Western Canada seems to be dependent on the early arrival of an abundant supply of wind-borne inoculum. In the medium rust years, wind-borne inoculum became plentiful considerably later than in the heavy rust years; and in the light rust years, with one exception, it was not abundant at all or only became abundant late in the season.

21. With respect to the length of time required for the wheat crop to mature, there was little or no difference between the heavy rust years and the light rust years. In the heavy rust years, however, seeding was usually a few days later than average, and, as infection appeared about the usual time and increased rapidly, the crop was subjected during most of its fruiting period to severe attack. In the medium rust years, moderate to severe infection only became established after the fruiting period of the bulk of the crop was about half or more completed.

22. The interrrelation of various factors influencing the development of stem rust in Western Canada is discussed, and an explanation is given in justification of the widely-held belief that a period of moist warm—"muggy"—weather is frequently a precursor of a heavy stem-rust attack.

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In the reorganization of the investigation in the autumn of 1925, some phases were much expanded, particularly the rust surveys and the slide-exposure studies. The Saskatoon Laboratory, in charge of Dr. Simmonds—

Dr. Fraser having in that year been appointed Professor of Biology in the University of Saskatchewan—assumed responsibility for rust surveys and overwintering studies in Saskatchewan and Alberta, and for the stationary slide exposures in those two provinces. In 1928, when the Dominion Laboratory of Plant Pathology was organized at Edmonton, Alta., under Dr. G. B. Sanford, that Laboratory undertook responsibility for the rust surveys in Alberta. The rust surveys made by the three Laboratories have been supplemented by the hearty co-operation of the Departments of Plant Pathology and of Agronomy of the Universities of the three Prairie Provinces. The Superintendents and Staffs of the several Dominion Experimental Farms in these provinces have also given valuable assistance, particularly in connection with the exposure of slides. Slide exposures on aeroplane flights were made possible by the kind assistance of the Committee on Civil Government Air Operation afforded through the excellent co-operation of the Branch of the Royal Canadian Air Force stationed at Winnipeg. Dr. J. Patterson, Controller, Meteorological Division, Air Services of Canada, kindly provided weather data that were unpublished or not readily accessible, and several of the Observers of this Division, in the three provinces, gladly assisted in the exposure of slides and in providing current weather observations. Mr. D. C. Archibald, of the same Division, has given helpful advice concerning certain meteorological aspects of the study. Much of the actual work involved in the surveys and slide examinations was performed by different members of the Staffs of the three plant pathological laboratories, particularly by Dr. B. J. Sallans of the Saskatoon Laboratory and Mr. Bjorn Peturson of the Winnipeg Laboratory, both of whom have contributed largely to the investigation. Mr. A. M. Brown kindly prepared the photographs. Grateful acknowledgment is made to these and all others who have assisted in the investigation; and to the Dominion Botanist, Dr. H. T. Güssow, under whose general supervision the work was carried on, for his constant interest and generous support.

REFERENCES

1. Abbott, E. V. Further notes on plant diseases in Peru. Phytopath. 21 : 1061-1071. 1931.

2. Aberhold, R. and W. Ruhland. Die Frage der Überwinterung und Verbreitung der Getreideroste. Mitt. Kais. Biolog. Anst. f. Land.-u. Forstwirtsch. Heft 2. 3-5. 1906.

3. Allen, Ruth R. A cytological study of infection of Baart and Kanred wheats by *Puccinia graminis tritici*. Jour. Agr. Res. 23 : 131-151. 1923.

4. Allen, Ruth R. Cytological studies of infection of Baart, Kanred, and Mindum wheats by *Puccinia graminis tritici* Forms III and XIX. Jour. Agr. Res. 26 : 571-604. 1923.

5. Appel, O. and A. Scheibe. Beobachtungen über die Verbreitung der einzelnen Getreiderosten in Deutschland, inbesondere im Jahre 1930. Mitt. Deutsch. Landw. Gesellsch. 46 : 61. 1931.

6. Arrhenius, O. Berberisbuskens förekomst i s. Stockholms län. Landtmannen 13 : 83. 1930.

7. Arthur, J. C. The plant rusts. Pp. 1-446. John Wiley & Sons, Inc., New York; Chapman & Hall, Ltd., London. 1929.

8. Asperger, K. Zur Frage der Überwinterung von *Puccinia triticina* Erikss. und *Puccinia graminis* Pers. in ihren Uredoformen. Zeitschr. Pflanzenkrank. 45 : 131-143. 1935.

9. ATKINS, I. M. Ecological factors in north Texas related to the 1935 stem rust epidemic. U.S. Dept. Agr., Plant Dis. Reptr., Sup. 93 : 31-41. 1936. (Mimeographed.)

10. BAILEY, D. L. The epidemiology of cereal rusts in Manitoba. *In* Report of the Dominion Botanist for 1924. Canada Dept. Agr. Ottawa, 42-43. 1925.

11. BANKS, JOSEPH. An account of the mildew. Ann. Agr. 43 : 514-527. 1805.

12. BAUDYS, E. Phytopathological notes VI. Abst. *in* Rev. Appl. Mycol. 10 : 295-296. 1931.

13. BEAUVERIE, J. On the development of wheat rusts in relation to climatic conditions. Rept. Intern. Conf. Phytopath. & Econ. Ent., Holland, 1923. 201-203. 1923.

14. BEAUVERIE, J. Sur les rapports existant entre le developpement des rouilles du blé et le climat. Compt. Rend. Acad. d. Sci. 176 : 529-531. 1923.

15 BEAUVERIE, J. Sur la germination des urédiospores des rouilles du blé. Compt. Compt. Rend. Acad. d. Sci. 179 : 993-996. 1924.

16. BEDFORD, S. E. Report of Experimental Farm for Manitoba. *In* Canada Dept. Agr. Exp. Farms Eept., Ottawa, 1896. 321-376. 1897.

17. BEDFORD, S. E. Report of Experimental Farm for Manitoba. *In* Canada Dept. Agr. Exp. Farms Rept., Ottawa. 1902. 279-318. 1903.

18. BENSAUDE, MATHILDE. Notes on wheat diseases in Portugal. Abst. *in* Rev. Appl. Mycol. 8 : 637-638. 1929.

19. BENSAUDE, MATHILDE. Black rust of cereals. Abst. *in* Rev. Appl. Mycol. 9 : 704-705. 1930.

20. BENSAUDE, MATHILDE. (Discussion on dissemination of cereal rusts). Proc. 5th Intern. Bot. Cong. Cambridge, 1930. 416. 1931.

21. BOLLEY, H. L. A preliminary report upon the relation of time of seeding and period of development to the development of rusts and smuts of oats. Proc. 17th Ann. Meet. Soc. Promotion Agr. Sci. 1896. 70-75. 1896.

22. BOLLEY, H. L. Einige Bemerkungen über die symbiotische Mykoplasmatheorie bei dem Getreiderost. Centralbl. f. Bakt. II. 4 : 887-896. 1898.

23. BOLLEY, H. L. Cause of wheat rust, its method of attack, conditions favourable to infection and rust development, and what to do. North Dakota Agr. Exp. Sta. Press Bull. 20. 1904.

24. BOLLEY, H. L. and F. J. PRITCHARD. Rust problems. Facts, observations and theories. Possible means of control. North Dakota Agr. Exp. Sta. Bull 68. 1906.

25. BRACKEN, J. Lessons from the rust epidemic of 1916. Saskatchewan Dept. Agr. Bull. 50. 1917.

26. BREGA, C. Further observations on the effect of the date of sowing upon the development of cereal rust. Abst. *in* Rev. Appl. Mycol. 8 : 93. 1929.

27. BROADBENT, W. H. Report of the barberry and the black rust of wheat survey in southwest Wales. Great Britain Jour. Min. Agr. 28 : 117-123. 1921.

28. BRUSCHETTI, C. On the germinative capacity of the uredospores of wheat rusts. Abst. *in* Rev. Appl. Mycol. 12 : 498. 1933.

29. BULLER, A. H. R. Essays on wheat. Pp. 1-339. MacMillan Co., New York. 1919.

30. BURTON, G. J. L. (Discussion on dissemination of cereal rusts). Proc. 5th Intern. Bot. Cong. Cambridge, 1930. 415. 1931.

31. BUTLER, E. J. The Indian wheat rust problem. India Dept. Agr. Bull. 1. 1903.

32. BUTLER, E. J. and J. M. HAYMAN. Indian wheat rusts. Mem. Dept. Agr. India, Bot. Ser. 1 : 1-52. 1906.

33. CARLETON, M. A. Cereal rusts in the United States. U.S. Dept. Agr. Bull. 16. 1899.

34. CARLETON, M. A. Lessons from the grain rust epidemic of 1904. U.S. Dept. Agr. Farmers' Bull. 219. 1905.

35. CASSELL, R. C. Effect of temperature on urediospore germination and germ tube development of five physiologic races of *Puccinia graminis tritici*. Phytopath. 29 : 4. 1939.

36. CASSELL, R. C. Effect of temperature on infection and development of eight physiologic races of *Puccinia graminis tritici* on wheat seedlings. Phytopath. 29 : 4. 1939.

37. CHABROLIN, C. La rouille noire du blé en Tunisie. Rev. Path. vég. et Ent. agr. 16 : 49-58. 1929.

38. CHATTERJEE, G. A note on an apparatus for catching spores from the upper air. Indian Jour. Agr. Sci. 1 : 306-308. 1931.

39. CHRISTMAN, A. H. Observations on the wintering of grain rusts. Trans. Wisconsin Acad. Sci. Arts & Letters. 15 : 98-107. 1904. (Pub'd. 1905).

40. COBB, N. A. Contributions to an economic knowledge of Australian rusts (Uredineae). Agr. Gaz. New South Wales 3 : 181-212. 1892.

41. CONNERS, I. L. Barberry (or *Berberis*). *In* Ann. Rept. Can. Plant Dis. Survey for years 1933 to 1940. Canada Dept. Agr., Ottawa, p. 65, 1933; 80, 1934; 65, 1935; 72, 1936; 72, 1937; 98, 1938; 101, 1939; 89, 1940.

42. CORNELLI, E. Notes on the development of rusts of wheat. Rev. Appl. Mycol. 12 : 497. 1933.

43. COTTON, A. D. Report on the occurrence of fungus, bacterial and allied diseases on crops in England and Wales for the years 1920-1921. Ministry of Agriculture and Fisheries (London), Misc. Pub. 38. 1922.

44. CRAIGIE, J. H. Economic diseases of field crops in Manitoba. Economic Survey Board, Province of Manitoba. 1939.

45. CRAIGIE, J. H. Aerial dissemination of plant pathogens. Proc. Sixth Pacific Sci. Cong. Berkeley and Palo Alto, Calif. 1939. 4 : 753-767. 1940.

46. CREPIN, C. Observations sur les rouilles des cereales en 1924 à Grignon. Rev. Path. vég. et Ent. agr. 11 : 317-320. 1924.

47. CREPIN, C. Note sur la rouille noire. Compt. Rend. Acad. Agr. France, 17 : 734-739. 1931.

48. CUNNINGHAM, G. H. The rust fungi of New Zealand. Pp. 1-261. John McIndoe, Dunedin, N.Z. 1931.

49. DARWIN, CHARLES. Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. *Beagle* round the world. 4th ed., pp. 1-381. Ward Lock & Co., London, New York, and Melbourne. 1889.

50. DAWSON, W. J. Some problems of economic biology in East Africa (Kenya Colony). Ann. Appl. Biol. 8 : 83-100. 1921.

51. DE BARY, A. Neue Untersuchungen über die Uredineen, insbesondere die Entwickelung der *Puccinia graminis* und der Zugammenhang derselben mit *Aecidium berberis.* Monatsber. der Akad. der Wissen. Berlin. Sitz. 12 : 15-50. 1865.

52. DODOFF, D. N. Die epidemische Entwicklung der Weizenroste in Nordbulgarien im Jahre 1932. Phytopath. Zeitschr. 6 : 111-112. 1933.

53. D'OLIVEIRA, B. Aspectos actuais do problema das ferrugens. Palestras agron. 2 : 5-77. 1940.

54. DUCOMET, V. Pathologie végétale. Pp. 1-298. (Librairie des Sciences agricoles. Charles Amat, Editeur, 11 rue de Mazieres). Paris. 1908.

55. DUCOMET, V. Les rouilles des cereales en automme et en hiver. Rev. Path. vég. et Ent. agr. 12 : 21-27. 1925.

56. DUCOMET, V. Les rouilles du blé au cours de la compagne 1925-1926. Rev. Path. veg. et Ent. agr. 14 : 39-44. 1927.

57. DURRELL, W. L. and E. A. LUNGREN. Barberry eradication and sources of black stem rust in Colorado. Colorado Agr. Exp. Sta. Bull. 315. 1927.

58. DURRELL, W. E. and J. H. PARKER. Comparative resistance of varieties of oats to crown and stem rusts. Iowa Agr. Exp. Sta. Res. Bull. 62. 1920.

59. ERIKSSON, J. and E. HENNING. Die Getreideroste, ihre Geschichte, Natur, sowie Massregeln gegen dieselben., pp. 1-463. P. A. Norstadt & Söner, Stockholm. 1896.

60. FERDINANDSEN, C. The campaign against *Berberis* in Denmark and its results. Abst. *in* Rev. Appl. Mycol. 4 : 268. 1925.

61. Foëx, Et. Rouilles des céréales., pp. 1-116. Coulet et Fils, Montpellier. 1908.

62. Foëx, Et., Mlle. Gaudineau, and M. Guyot. Les rouilles des cereales en 1923 et 1924 dans région parisienne. Rev. Path. vég. et Ent. agr. 11 : 198-211. 1924.

63. Forward, D. F. The influence of altered host metabolism upon modification of the infection type with *Puccinia graminis tritici* form 21. Phytopath. 22 : 493-555. 1932.

64. Fraser, W. P. The cereal rusts. Ann. Rept. Quebec Soc. Protect. Plants, 1914-15. 116-120. 1915.

65. Fraser, W. P. The outbreak of wheat rust in 1916. Month. Bull. Agr. Statist. Dept. Trade and Commerce, Ottawa, Canada. 11 : 61-67. 1918.

66. Fraser, W. P. Wintering over of the urediniospores of stem rust. *In* Reports of the Dominion Botantist for the years 1921, 1922, 1923. Canada Dept. Agr., Ottawa, 1921, 1922, 1923.

67. Freeman, E. M. and E. C. Johnson. The rusts of grain in the United States. U.S. Dept. Agr. Bull. 216. 1911.

68. Friedrichson, G. A. Wheat rust in the irrigated districts of the Trans-Volga Region. Abst. *in* Rev. Appl. Mycol. 16 : 661-662. 1937.

69. Garbowski, L. and H. Juraszkowna. Essais d'identification des formes biologiques de la rouille *Puccinia graminis tritici*, provenant du territoire de Pologne. (Note preliminaire). Rev. Path. vég. et Ent. agr. 21 : 45-55. 1934.

70. Gassner, G. Die Getreideroste und ihr. Auftreten im subtropischen östilichen Sudamerika. Centralbl. f. Bakt. II. 44 : 305-381. 1915.

71. Gassner, G. Untersuchungen über die Abhängigkeit des Auftretens der Getriede-roste vom Entwicklungszustand der Nahrpflanze und von äusseren Faktoren. Centralbl. f. Bakt. II. 44 : 512-617. 1915.

72. Gassner, G. Beiträge zur Frage der Überwinterung und Verbreitung der Getreide-roste im subtropischen Klima. Zeitschr. f. Pflanzenkrank. 26 : 329-374. 1916.

73. Gassner, G. Neue Festellungen über Auftreten und Verbreitung der Getreiderost-arten in Südamerika. Phytopath. Zeitschr. 4 : 189-203. 1931.

74. Gassner, G. Uber Verschiebung der Rostresistenz während der Entwicklung der Getreidepflanzen. Phytopath. Zeitschr. 4 : 549-596. 1932.

75. Gassner, G. and E. Pieschel. Untersuchungen zur Frage der Uredoüberwinterung der Getreideroste in Deutschland. Phytopath. Zeitschr. 7 : 355-392. 1934.

76. Gassner, G. and W. Straib. Untersuchungen über die Infektionsbedingungen von *Puccinia glumarum* und *Puccinia graminis*. Arb. Biol. Reichsanst. 16 : 609-629. 1928.

77. Gonzala, F. R. Cereal rusts. Abst. *in* Rev. Appl. Mycol. 5 : 658. 1926.

78. Goulden, C. H., M. Newton, and A. M. Brown. The reaction of wheat varieties at two stages of maturity to sixteen physiologic forms of *Puccinia graminis tritici*. Sci. Agr. 11 : 9-25. 1930.

79. Greaney, F. J. Cereal rust losses in Western Canada. Sci. Agr. 16 : 608-613. 1936.

80. Hansen, H. R. Severity of attacks of black stem rust in Denmark 1887-1921. Phytopath. 13 : 404-407. 1923.

81. Hart, Helen. Relation of stomatal behaviour to stem-rust resistance in wheat. Jour. Agr. Res. 39 : 929-948. 1929.

82. Hart, Helen and I. L. Forbes. The effect of light on the initiation of rust infection. Phytopath. 25 : 715-725. 1935.

83. Hart, Helen and Karol Zaleski. The effect of light intensity and temperature on infection of Hope wheat by *Puccinia graminis tritici*. Phytopath. 25 : 1041-1066. 1935.

84. Harter, L. L. Podblight of the lima bean caused by *Diaporthe phaseolorum*. Jour. Agr. Res. 11 : 473-504. 1917.

85. Heald, F. D. Manual of Plant Diseases. Pp. 1-891. McGraw-Hill Book Co., Inc., New York. 1926.

86. HEMMI, T. On the distribution of cereal rusts in Japan and the relation of humidity to germination of urediniospores of some species of *Puccinia*. Proc. 5th Pacific Sci. Cong., Canada, 1933. 4 : 3187-3194. 1934.

87. HENNING, E. Lagstiftningen mot Berberis busken med särskild hänsyn till frågans nuvarande läge i vårt land. Tidskr. f. Landtman 37 : 1-15. 1916.

88. HENNING, E. Den norske berberislagen och dess forhistoria. Landtmannen; tidskrift for Sveriges jordbruk och dess binaringer. 27 (42) : 377-379. October 21, 1916.

89. HENNING, E. Predisponerande betingelser för svartrosthärjningar. Landtmannen; tidskrift för landtman. 9 (51) : 1023-1025 and 9 (52) : 1041-1043. December 18 and 25, 1926.

90. HILTNER, L. Der Schwartzrost des Getreides und die Berberitze. Flugblätter zur Förderung des Pflanzenbaues und des Pflanzenschutzes No. 36. May, 1920.

91. HITCHCOCK, A. S. and M. A. CARLETON. Second report on rusts of grain. Kansas Agr. Coll. Exp. Sta. Bull. 46. 1894.

92. HUMPHREY, H. B. Notes on incidence of cereal rusts, crop season 1937. U.S. Dept. Agr., Plant Disease Reporter 21 : 305-306. 1937. (Mimeographed).

93. HUMPHREY, H. B. Relation of upper-air mass movement to incidence of stem rust. Phytopath. 28 : 10. 1938.

94. HUMPHREY, H. B., E. C. STAKMAN, E. B. MAINS, C. O. JOHNSTON, H. C. MURPHY and W. M. BEVER. The rusts of cereal crops. U.S. Dept. Agr. Circ. 341. 1935

95. HURST, R. R. Cereal rust investigations. *In* Report of the Dominion Botanist for 1926. Canada Dept. Agr., Ottawa. 1927.

96. HUTCHESON, T. B. and K. E. QUANTZ. The effect of greenhouse temperatures on the growth of small grains. Jour. Amer. Soc. Agron. 9 : 17-21. 1917.

97. HWANG, L. The effect of light and temperature on the viability of urediospores of certain cereal rusts. Phytopath. 32 : 699-711. 1942.

98. JACKSON, V. W. Rusts and smuts of grain crops. Manitoba Dept. Agr. and Immigration. Extension Bull. 44. 1919.

99. JACKSON, V. W., W. P. FRASER, and D. L. BAILEY. The present status of the barberry eradication in Western Canada. Sci. Agr. 5 : 375-378. 1925.

100. JACZEWSKI, A. Studien über das Verhalten des Schwartzrostes des Getreides in Russland. Zeitschr. f. Pflanzenkrank. 20 : 321-359. 1910.

101. JENKIN, T. J. and KATHLEEN SAMPSON. Rust resistant trials with wheat. Welsh Plant-Breeding Sta. Bull. Ser. C. 1 : 41-49. 1921.

102. JOHNSON, A. G. AND J. G. DICKSON. Stem rust of grains and the barberry in Wisconsin. Wis. Agr. Exp. Sta. Bull. 304. 1919.

103. JOHNSON, E. C. Cardinal temperatures for the germination of uredospores of cereal rusts. Phytopath. 2 : 47. 1912.

104. JOHNSON, T. and M. NEWTON. The effect of high temperatures on the uredial development in cereal rusts. Can. Jour. Res. C, 15 : 425-432. 1937.

105. JOHNSON, T. and M. NEWTON. The influence of light and certain other environmental factors on the mature-plant resistance of Hope wheat to stem rust. Can. Jour. Res. C, 18 : 357-371. 1940.

106. JOHNSTON, C. O., L. E. MELCHERS, H. H. LAUDE, and J. H. PARKER. The stem rust epidemic of 1935 in Kansas. U.S. Dept. Agr., Plant Dis. Reptr., Suppl. 92 : 19-30. 1936. (Mimeographed).

107. JOHNSTON, C. O., L. E. MELCHERS, and J. O. MILLAR. The stem-rust epidemic of 1937 in Kansas. U.S. Dept. Agr., Plant Dis. Reptr. Suppl. 107. 83-94. 1938.

108. KEMPTON, F. E. Progress of barberry eradication. U.S. Dept. Agr. Circ. 188, 1921.

109. KIKOINA, R. Wheat rust in the Azoff-Black Sea and North Caucasus regions, and their control. Abst. *in* Rev. App. Mycol. 15 : 785. 1936.

110. KLEBAHN, H. Beiträge zur Kenntnis der Getreideroste. II. Zeitsch. f. Pflanzenkrank, 10 : 70-96. 1900.

111. KLEBAHN, H. Die wirtswechselnden Rostpilze. Pp. 1-447. Gebrüder Borntraeger, Berlin. 1904.

112. LAGERHEIM, G. Ueber das Vorkommen von europiäschen Uredineen auf der Hochebene von Quito. Botanisches Centralblatt 54 : 324-377. 1893.

113. LAMBERT, E. B. The relation of weather to the development of stem rust in the Mississippi Valley. Phytopath. 19 : 1-71. 1929.

114. LATHBURY, R. J. Report of Acting Senior Plant Breeder. Kenya Dept. Agr Rept. 1933. 182-200. 1934.

115. LAURITZEN, J. I. The relation of temperature and humidity to infection by certain fungi. Phytopath. 9 : 7-35. 1919.

116. LEHMANN, E., A. BADER, G. MITTMAN, and O. SCHNITZLER. Berberitzenverbreitung und Schwarzrostauftreten in Württenburg. Landw. Jahreb. 80 : 1. 1-37. 1934.

117. LEHMANN, E., H. KUMMER, and H. DANNEMANN. Der Schwarzrost seine Biologie und seine Bekämpfung in Verbindung mit der Berberitzenfrage. pp. 1-584. J. F. Lehmann, München and Berlin. 1937.

118. LEVINE, M. N. Biometrical studies on the variation of physiologic forms of *Puccinia graminis tritici* and the effects of ecological factors on the susceptibility of wheat varieties. Phytopath. 18 : 7-124. 1928.

119. LIND, J. Effect of destruction of the barberry (*Berberis vulgaris*) on the common rust of wheat (*Puccinia graminis*) in Denmark. Intern. Rev. Sci. Prac. Agr. 7 : 442. 1915.

120. LIND, J. Berberisbusken og Berberisloven. Tidsskr. for Planteavl. 22 : 729-780. 1915.

121. LINDFORS, T. Berberisutrotningen i Sverige. Landtmann 9 : 412-413. 1926.

122. LOFTFIELD, J. V. G. The behaviour of stomata. Carnegie Inst. Wash. Pub. 314. Washington, D.C. 1921.

123. MARTIN, F. J. and R. E. MASSEY. Experiments on wheat growing in the Sudan. Wellcome Tropical Research Laboratories, Chemical Section, Publication No. 19, Khartoum, 1921.

124. MATTRAS, H. Observations sur les rouilles du blé faires à Versailles en 1931 et 1932. Ann. des Epiphytes 18 : 384-397. 1932.

125. MAXIMOV, N. A. and L. K. Zernova. Behaviour of stomata of irrigated wheat plants. Plant Physiology 11 : 651-654. 1936.

126. MAXWELL, IRIS and G. B. WALLACE. Black rust in Scotland. Trans. Brit. Mycol. Soc. 11 : 138-145. 1926.

127. MCALPINE, D. The life-history of the rust of wheat. Victoria Dept. Agr. Bull. 14, 1891.

128. MCALPINE, D. The rusts of Australia. Pp. 1-349. Melbourne, Australia. 1906.

129. MCKILLICAN, W. C. Experiments with wheat at the Dominion Experimental Farm, Brandon, Manitoba. A survey 1889-1923. Canada Dept. Agr. Bull 42. N.S. 1924.

130. MEHTA, K. C. Observations and experiments on cereal rusts in the neighbourhood of Cambridge, with special reference to their annual recurrence. Trans. Brit. Mycol. Soc. 8 : 142-176. 1923.

131. MEHTA, K. C. Annual recurrence of rusts on wheat in India. Proc. Indian Sci. Cong. 16 : 199-223. 1929.

132. MEHTA, K. C. Annual outbreaks of rust on wheat and barley in the Plains of India. Indian Jour. Agr. Sci. 1 : 297-301. 1931; Proc. 5th Intern. Bot. Cong., Cambridge, 1930. 413-414. 1931.

133. MEHTA, K. C. (Discussion on dissemination of cereal rusts.) Proc. 5th Intern. Bot. Cong., Cambridge, 1930. 415, 1931.

134. MEHTA, K. C. Rusts of wheat and barley in India. A study of their annual recurrence, life-histories, and physiologic forms. Indian Jour. Agr. Sci. 3 : 939-962. 1933.

135. MEHTA, K. C. Further studies on cereal rusts in India. Sci. Monogr. Coun. Agr. Res. India, 14. Pp. 1-224. Government of India Press, Calcutta. 1940.

136. MEIER, F. C., J. A. STEVENSON, and V. K. CHARLES. Spores in the upper air. Phytopath. 23 : 23. 1933.

137. MELANDER, L. W. Effect of temperature and light on development of the uredial stage of *Puccinia graminis*. Phytopath. 21 : 109. 1931; Jour. Agr. Res. 50 : 861-880. 1935.

138. MELCHERS, L. E. Plant disease problems in Egypt. Trans. Kansas Acad. Sci. 35 : 39-61. 1932.

139. MELCHERS, L. E. The wheat stem rust epidemic of Kansas in 1940. U.S. Dept. Agr., Plant Dis. Reptr. Suppl. 132 : 95-103. 1941. (Mimeographed).

140. MELCHERS, L. E. and C. O. JOHNSTON. The wheat stem and leaf rust epidemics of 1938 in Kansas. U.S. Dept. Agr., Plant Dis. Reptr. Suppl. 116 : 51-68. 1939. (Mimeographed).

141. MELHUS, I. E., W. L. DURRELL and R. S. KIRBY. Relation of the barberry to stem rust in Iowa. Iowa Agr. Exp. Sta. Res. Bull. 57 : 283-325. 1920.

142. MOREAU, M. F. Les maladies des céréales à la station de sélection de semences du massif Central en 1924. Rev. Path. vég. et Ent. agr. 12 : 31-37. 1925.

143. MORELAND, W. H. The relation of the weather to rust on cereals. Mem. Dept. Agr. India, Bot. Ser. 1 : 53-58. 1906.

144. MORRIS, H. E. and W. L. POPHAM. The barberry eradication campaign in Montana. Mont. Agr. Exp. Sta. Bull. 180. 1925.

145. MURPHY, P. A. (Discussion on dissemination of cereal rusts.) Proc. 5th Intern. Bot. Cong. Cambridge, 1930. 416-417. 1931.

146. NEWTON, MARGARET. The cereal rusts in Canada. Emp. Jour. Exp. Res. 6 : 125-140. 1938.

147. NEWTON, MARGARET and A. M. BROWN. Studies on the nature of disease resistance in cereals. I. The reactions to rust of mature and immature tissues. Can. Jour. Res. 11 : 564-581. 1934.

148. NEWTON, MARGARET and T. JOHNSON. Specialization and hybridization of wheat stem rust, *Puccinia graminis tritici*, in Canada. Canada Dept. Agr. Bull. 160. N.S. 1932.

149. PAMMEL, L. H. The barberry in Iowa and adjacent states. Proc. Iowa Acad. Sci. 26 : 193-237. 1919.

150. PELTIER, G. L. A study of the environmental conditions influencing the development of stem rust in the absence of an alternate host. I. The viability of the urediniospores of *Puccinia graminis tritici* form 3. Nebraska Agr. Exp. Sta. Res. Bull. 22. 1922.

151. PELTIER G. L. A study of the environmental conditions influencing the development of stem rust in the absence of an alternate host. II. Infection studies with *Puccinia graminis tritici* form 3 and form 9. Nebraska Agr. Exp. Sta. Res. Bull. 25. 1923.

152. PELTIER, G. L. A study of the environmental conditions influencing the development of stem rust in the absence of an alternate host. III. Further studies on the viability of the urediniospores of *Puccinia graminis tritici*. Nebraska Agr. Exp. Sta. Res. Bull. 34. 1925.

153. PELTIER, G. L. A study of the environmental conditions influencing the development of stem rust in the absence of an alternate host. IV. Overwintering of urediniospores of *Puccinia graminis tritici*. Nebraska Agr. Exp. Sta. Res. Bull. 35. 1925.

154. PELTIER, G. L. A study of the environmental conditions influencing the development of stem rust in the absence of an alternate host. V. The period of initial infection of urediniospores of *Puccinia graminis tritici* on wheat. Nebraska Agr. Exp. Sta. Res. Bull. 35. 1925.

155. PELTIER, G. L. A study of the environmental conditions influencing the development of stem rust in the absence of an alternate host. VI. Influence of light on infection and subsequent development of urediniospores of *Puccinia graminis tritici* on wheat. Nebraska Agr. Exp. Sta. Res. Bull. 35. 1925.

156. PELTIER, G. L. Some aspects of the spread of stem rust. Centralbl. f. Bakt. II. 78 : 525-535. 1929.

157. PELTIER, G. L. Relation of weather to the prevalence of wheat stem rust in Nebraska. Jour. Agr. Res. 46 : 59-73. 1933.

158. PELTIER, G. L. and A. F. THIEL. Stem rust in Nebraska. Nebr. Agr. Exp. Sta. Res. Bull. 42. 1927.

159. PETERSON, R. F. Stomatal behaviour in relation to the breeding of wheat for resistance to stem rust. Sci. Agr. 12 : 155-173. 1931.

160. PETIT, A. De la transmission des rouilles des céréales en Tunisie. Ann. du Service Bot. de Tunisie 7 : 111-130. 1931.

161. PETIT, A. La transmission et le traitement des rouilles des céréales en Tunisie. Ann. du Service Bot. Agron. de Tunisie 9 : 201-218. 1932.

162. PETURSON, B. Epidemiology of cereal rusts. *In* Rept. of the Dominion Botanist for 1930: 44-46. Canada Dept. Agr. Ottawa. 1931.

163. PHILP, JAMES and A. G. SELIM. Rust-resistant wheats for Egypt. Nature 147 : 209. 1941.

164. POTENZA, G. Observations on the susceptibility of cereals to rust. Abst. *in* Rev. Appl. Mycol. 8 : 759-761. 1929.

165. PRITCHARD, F. J. A preliminary report on the yearly origin and dissemination of *Puccinia graminis*. Bot. Gaz. 52 : 169-192. 1911.

166. PROCTOR, B. E. The microbiology of the upper air. I. Proc. Am. Acad. Arts, Sci. 69 : 315-340. 1934.

167. PROCTOR, B. E. The microbiology of the upper air. II. Jour. Bacteriology 30 : 363-375. 1935.

168. RAEDER, J. M. and W. M. BEVER. Spore germination of *Puccinia glumarum* with notes on related species. Phytopath. 21 : 767-789. 1931.

169. REDDY, W. F. Black stem rust situation in Michigan. Mich. Quart. Bull. Agr. Exp. Sta. 8 : 148-151. 1926.

170. ROUSSAKOV, L. F. Observations sur l'influence des conditions météorologiques sur de développement de la rouille des céréales. Rept. Intern. Conf. Phytopath. and Econ. Ent., Holland, 1923. 227-280. 1923.

171. ROUSSAKOV, L. F. Peculiarities of the microclimate in the midst of plants in connection with the development of cereal rusts. Abst. *in* Rev. Appl. Mycol. 4 : 471-473. 1925.

172. ROUSSAKOV, L. F. Some results of the survey of cereal rusts in 1922-1924. Abst. *in* Rev. Appl. Mycol. 5 : 724. 1926.

173. ROUSSAKOV, L. F. Cereal rust in the Far East according to the data obtained from an enquiry in 1925. Abst. *in* Rev. Appl. Mycol. 7 : 232-233. 1928.

174. ROUSSAKOV, L. F. and M. F. PANTCHENKO. Infection of 1290 pure lines of wheat with stem rust and conception of immunity in time. Abst. *in* Rev. Appl. Mycol. 8 : 362-363. 1929.

175. RUDORF, W. and MARIA JOB. Unteruschungen bezüglich der Spezialisierung von *Puccinia graminis tritici*, *Puccinia triticina* und *Puccinia glumarum tritici*, sowie über Resistenz und ihre Vererbung in verschiedenen Kreuzungen. Zeitschr. f. Züchtung, A, 19 : 333-365. 1934.

176. RUSSELL, H. L., F. B. MORRISON, and W. H. EBLING. Gleanings from Science. Ann. Rept. Wisconsin Agr. Exp. Sta. Bull. 388. 1926.

177. SAVULESCU, T. Rumania: Black rust of cereals in 1932 and measures taken to prevent future outbreaks. Intern. Rev. Agr. 24 : No. 2. (Plant Protection) 29-31. 1933.

178. SAVULESCU, T. Beitrag zur Kenntnis der Biologie der Puccinia-Arten, die den Weizen in Rumanien befallen. Zeitschr. f. Pflanzenkrank. u. Pflanzenschutz. 43 : 577-594. 1933.

179. SAVULESCU, T. The problem of wheat rusts in Rumania in its relation to Central Europe. Abst. *in* Rev. Appl. Mycol. 17 : 510-511. 1938.

180. SCHAFFNIT, E. Studien über den Einfluss niederer Temperaturen auf die pflanzliche Zelle. Mitt. Kaiser-Wilhelm Inst. f. Landw. Bromberg 3 : 93-144. 1910.

181. SCHEIBE, A. Die Schwarzrostepidemie auf dem Balkan 1932. Nachrichtenbl. Deutsch Pflanzenschutzdienst 13 : 5-6. 1933.

182. SCHILBERSZKY, K. Der Berberitzenstrauch und die Schwarzrostfrage. Phytopath. Zeitschr. 2 : 614-637. 1930.

183. SHITIKOVA-ROUSSAKOVA, A. On the question of how rust infection is introduced into the AmurRegion. Abst. *in* Rev. Appl. Mycol. 7 : 233-235. 1928.

184. SIBILIA, C. Researches on cereal rusts. Abst. *in* Rev. Appl. Mycol. 8 : 162-163. 1929.

185. Sibilia, C. The distribution of *Berberis* in Italy in relation to *Puccinia graminis* Pers. Abst. *in* Rev. Appl. Mycol. 16 : 89. 1937.

186. Sibilia, C. Researches on cereal rusts. VII. The overwintering of *Puccinia graminis tritici* Erikss. & Henn. and *P. triticina* Erikss. in Italy. Abst. *in* Rev. Appl. Mycol. 16 : 593. 1937.

187. Siemaszko, W. Quelques observations sur les maladies des plantes en Pologne. Rev. Path. vég. Ent. agr. 20 : 139-147. 1933.

188. Sorauer, P. Vorarbeiten für eine internationale Statistik der Getreideroste. Zeitschr. f. Pflanzenkrank. 19 : 193-286. 1909.

189. Stakman, E. C. The black stem rust and the barberry. U.S. Dept. Agr. Year Book, 1918. 75-100. 1919.

190. Stakman, E. C. Barberry eradication prevents black stem rust in Western Europe. U.S. Dept. Agr., Dept. Circ. 269. 1923.

191. Stakman, E. C. Destroy the common barberry. U.S. Dept. Agr. Farmers' Bull. 1058, 1919 and 1923.

192. Stakman, E. C. The dissemination of cereal rusts. Proc. 5th Intern. Bot. Cong., Cambridge, 1930. 411-413. 1931.

193. Stakman, E. C. Epidemiology of cereal rusts. Proc. 5th Pacific Sci. Cong., Victoria and Vancouver, Canada, 1933. 4 : 3177-3184. 1934.

194. Stakman, E. C. Stem rust of cereals. U.S. Dept. Agr., Plant Disease Reporter 19 : 153-154. 1935. (Mimeographed).

195. Stakman, E. C. The 1935 black stem rust epidemic. The Northwestern Miller 184 : 62. 1935.

196. Stakman, E. C. Preliminary data relating to the development of stem rust in 1937. U.S. Dept. Agr., Plant Dis. Reptr. 21 : 238-239. 1937. (Mimeographed).

197. Stakman, E. C. Further estimates on probable stem rust damage this year. U.S. Dept. Agr., Plant Disease Reporter 22 : 336-337. 1938. (Mimeographed).

198. Stakman, E. C. Wind dissemination of plant pathogens. Proc. 3rd Intern. Cong. Microbiol., New York, 1939. 272-273. 1940.

199. Stakman, E. C., W. T. Butler, R. U. Cotter, and J. J. Christensen. The epidemiology of stem rust of wheat in three successive contrasting years. Phytopath. 28 : 20. 1938.

200. Stakman, E. C. and R. C. Cassell. The increase and importance of Race 56 of *Puccinia graminis tritici*. Phytopath. 28 : 20. 1938.

201. Stakman, E., R. C. Cassell, and W. Q. Loegering. Population trends of physiologic races of *Puccinia graminis tritici* in the United States from 1930 to 1939. Phytopath. 30 : 22-23. 1940.

202. Stakman, E. C. and L. H. Hamilton. Stem rust in 1938. U.S. Dept. Agr., Plant Dis. Reptr. Suppl. 117 : 69-83. 1939. (Mimeographed).

203. Stakman, E. C., A. W. Henry, G. C. Curran, and W. N. Christopher. Spores in the upper air. Jour. Agr. Res. 24 : 599-605. 1923.

204. Stakman, E. C., Lee Hines, R. C. Cassell, and M. N. Levine. Population trends of physiologic forms of *Puccinia graminis tritici*, 1930 to 1934. Phytopath. 25 : 34. 1935.

205. Stakman, E. C., F. E. Kempton, and L. D. Hutton. The common barberry and black stem rust. U.S. Dept. Agr. Farmers' Bull. 1544. 1927.

206. Stakman, E. C., R. S. Kirby, and A. F. Thiel. The regional occurrence of *Puccinia graminis* on barberry. Phytopath. 11 : 39-40. 1921.

207. Stakman, E. C. and E. B. Lambert. The relation of temperature during the growing season in the spring wheat area of the United States to the occurrence of stem-rust epidemics. Phytopath. 18 : 369-374. 1928.

208. STAKMAN, E. C., and M. N. LEVINE. Effect of certain ecological factors on the morphology of the urediniospores of *Puccinia graminis*. Jour. Agr. Res. 16 : 43-77. 1919.

209. STAKMAN, E. C., M. N. LEVINE, and J. M. WALLACE. The value of physiologic-form surveys in the study of the epidemiology of stem rust. Phytopath. 19 : 951-959. 1929.

210. STAKMAN, E. C. and W. Q. LOEGERING. Physiologic races of *Puccinia graminis* in the United States in 1939. Paper No. 1840 of Sci. Jour. Series, Minn. Agr. Exp. Sta. Issued by U.S. Dept. Agr. Jan. 1941.

211. STAKMAN, E. C., L. W. MELANDER, and D. G. FLETCHER. Barberry eradication pays. Minnesota Dept. Agr. Bull. 55. 1927.

212. STAKMAN, E. C. and F. J. PIEMEISEL. Biologic forms of *Puccinia graminis* on cereals and grasses. Jour. Agr. Res. 10 : 429-495. 1917.

213. STAKMAN, E. C., W. L. POPHAM, and R. C. CASSELL. Observations on stem-rust epidemiology in Mexico. Phytopath. 29 : 22. 1939; Amer. Jour. Bot. 27 : 90-99. 1940.